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A COMPARATIVE STUDY OF WINTER AND SUMMER LEAVES OF VARIOUS HERBS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 224

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Introduction

The structure of most plants varies with the habitat and even with the varying conditions of the same habitat. This has been emphasized by GREVILLIUS,[1] CHERMEZON,[2] COWLES,[3] STARR,[4] and others. GREVILLIUS made an extensive comparative study of vegetation growing on the island Öland. He compared the plants of a dry, rocky, treeless plain (alvar) with the same species growing in favorable regions. The former he calls alvar forms; the latter, normal forms. The alvar forms, in general, were more hairy and had a more highly cutinized and thicker epidermal wall, a more compact palisade parenchyma, and more closely crowded stomata than the normal forms.

These structural peculiarities due to environmental changes may be observed readily in almost any plastic plant. *Oenothera*

[1] GREVILLIUS, A. Y., Morphologisch-anatomische Studien über die xerophile Phanerogamenvegetation der Insel Öland. Bot. Jahrb. **23**:24–108. 1897.

[2] CHERMEZON, H., Recherches anatomiques sur les plantes littorales. Ann. Sci. Nat. Bot. **12**:117–313. 1910.

[3] COWLES, H. C., The ecological relation of the vegetation of the sand dunes of Lake Michigan. BOT. GAZ. **27**:95–117, 167–202, 281–308, 361–391. 1899.

[4] STARR, ANNA M., Comparative anatomy of dune plants. BOT. GAZ. **54**: 295–305. 1912.

biennis, for example, when growing in a dry, sterile soil and exposed to strong wind and maximum sunlight, is found to have smaller and thicker leaves, more perfectly developed palisade parenchyma, a more hairy and a more densely cutinized epidermis, and, in general, a more xerophytic structure than the same species growing under more favorable conditions.

A similar structural difference is apparent in summer and winter leaves, or in stem and rosette leaves. Winter leaves, as the name implies, exist during the winter, which, in our latitude, is the most unfavorable season of the year. During the winter transpiration becomes relatively excessive because of the reduced rate of absorption, and plants are thus put to the severest test. Sometimes for days at a time the ground is frozen and absorption is practically zero; while during the warmest part of the day considerable transpiration may take place. The plant is thus exposed to the danger of desiccation. Moreover, during the night the most exposed leaves may freeze hard. Toward noon of the following day they may thaw out, presenting a wilted condition as if killed by scalding. However, it is surprising how quickly such leaves will revive as conditions again become more favorable. No sooner is the absorption of soil water resumed than the leaves once more become turgid and resume their wonted appearance, apparently none the worse for the ordeal through which they have passed.

Since winter leaves are exposed to such severe conditions, it would be natural to suppose that they must be quite xerophytic in structure. While this is true to a certain extent, in some respects they are less exposed to unfavorable conditions than stem leaves. This is especially true of winter leaves occurring in rosettes. In rosettes the internodes are extremely short and the leaves thus become closely crowded and overlapping. Since epinasty prevails during the winter, these overlapping leaves lie almost flat on the ground, thus affording maximum protection for each other from sudden changes of temperature, as well as from high winds and excessive transpiration. It is seldom that winter leaves die as the direct result of freezing, and when it is borne in mind that such leaves have a low water content and a high osmotic pressure, thus insuring easier absorption of soil water, the protection would seem

ample, regardless of any special protective structures. The stem leaves, on the other hand, are usually borne some distance above the ground and exposed to greater intensity of light, stronger winds, and greater extremes in temperature, humidity, and transpiration.

Method of study

Most of the plants used in this comparative study were collected in the region about Chicago; the remainder, in eastern Pennsylvania. In order to simplify matters, all winter leaves, whether produced in typical rosettes, on prostrate runners, or on basal shoots, will be designated as rosette leaves, and summer leaves will be designated as cauline or stem leaves.

Leaves for study were killed, fixed, and preserved in a 4 per cent solution of formaldehyde in 50 per cent alcohol. Delafield's haematoxylin was used as a general staining reagent. Sections were also treated with chloriodide of zinc, the cellulose wall turning blue, while the cuticle and cutinized portions of the epidermal wall turned yellow. Alcannin tincture imparts a pink color to cutin, but is much slower in its action than chloriodide of zinc.

Unless otherwise specified, all observations were made on the middle of the leaf, from the midrib to the margin. All observations and measurements were made with $\frac{2}{3}$, $\frac{1}{6}$, and $\frac{1}{12}$ in. (oil immersion) objectives, and with a 1 in. micrometer eyepiece with divisions of 0.1 mm. Camera lucida drawings were made of portions of the epidermis for measurement and comparison of epidermal cells and stomata. Chloral hydrate was used as a clearing agent for leaves to facilitate the study of air spaces and packing of mesophyll tissues. Most measurements and counts represent an average of 5–20, depending upon the degree of variability of the objects measured. Measurements are expressed in microns, and counts represent the number in the field under low or high power, which is indicated in each case. Different plants of the same species (in cases where the plants could readily be secured) were studied at different times and the results compared. These results varied only slightly when the plants came from the same habitat, but usually differed considerably in plants from different habitats.

With such a tendency to variation in plants, few measurements and counts can be regarded as absolutely fixed, but the final results in any case do not materially affect the principles involved.

Epidermal hairs

There is considerable variation in the kind, number, size, and distribution of epidermal hairs, not only in different plants of the same species, but also on different leaves of the same plant, or even on different parts of the same leaf. Some plants, such as *Oenothera biennis*, vary greatly when grown under different physical conditions. In a low, moist, and comparatively shady habitat the leaves of *Oenothera* are thin, and the hairs rather weak and comparatively few and scattered. On a dry slope or bank along the roadside, the leaves are decidedly thicker, and the hairs stouter and very much more abundant; while under intermediate conditions corresponding variations have been observed.

Oenothera is an extremely plastic plant, responding readily to changed conditions of environment. *Leonurus Cardiaca*, *Lepidium virginicum*, *Capsella Bursa-pastoris*, and others also show some variations, but not to the same extent as *Oenothera*. *Verbascum Blattaria*, on the other hand, is glabrous no matter under what physical conditions it may be growing. Occasionally, when growing on a dry bank along a dusty roadside, a few hairs may be found on the ventral side of the midrib of the lower stem leaves and upper rosette leaves. This plant is extremely rigid and does not at all, or but slightly, yield to changing conditions of environment. It is perhaps a good illustration of a congenital mesophyte.

In studying the number and distribution of hairs, *Oenothera biennis*, *O. rhombipetala*, *Leonurus Cardiaca*, *Lepidium virginicum*, *Capsella Bursa-pastoris*, and *Hieracium paniculatum* were selected as types. Care was taken to collect both the stem and rosette plant of each species in the same or as nearly the same habitat as possible. Five plants of each species were studied, and the counts for each particular kind of hairs were averaged and tabulated. The field of the low power of the microscope was adopted as the unit area of observation, and the average of 5 or more counts was taken as the number for each area under observation.

From the tabulated results of observations made on these species of plants and a careful study of a number of other species, the following conclusions can be formulated. (1) Epidermal hairs are most abundant on the upper stem leaves, and decrease, as a rule, to the lowest stem leaves, and from the upper to the lowest rosette leaves. On the basal leaves of both stem and rosette are found the smallest number of hairs. (2) Hairs are also more abundant on the lower than on the upper surface of the leaf, usually being most abundant on the ribs, veins, and margin of the leaf. (3) Hairs are most abundant toward the base of leaves, although in basal stem and rosette leaves the reverse is usually the case. (4) Young leaves are more hairy than older ones. This may be due partly to the fact that in young immature leaves the epidermal cells have not yet reached their mature size and therefore the hairs will of necessity be more crowded than in a mature leaf. This diminished hairiness in older leaves also may be due in part to the fact that hairs in the course of time may break off, or for some reason or other drop off, and thus reduce the number per unit area of surface. (5) Exposure to sun, wind, and other desiccating influences tends to increase the hairiness in the upper stem leaves. Transpiration, wind, moisture, and character of soil are undoubtedly potent factors in determining hair production, but that these are not the only factors is clearly shown by the fact that young leaves just emerging from buds, and therefore most protected, are usually most hairy, sometimes even tomentose.

As stated before, some leaves are most hairy toward the base, where the leaf is most protected from those influences that would ordinarily tend to produce hairiness. It is difficult also to see why *Verbascum Thapsus* and *V. Blattaria* should grow side by side, the one glabrous and the other extremely hairy. So far as hairiness is concerned, it would seem that the former is a congenital xerophyte while the latter is a congenital mesophyte.

It is difficult also to see that hairiness is beneficial to plants, and that these epidermal outgrowths protect the plant against excessive transpiration, against the ravages of animals and parasites of various kinds, against excessive sunlight, etc., when *Verbascum Blattaria*, entirely devoid of hairs and with only a slightly

thicker epidermal wall, is fully as successful in the struggle for existence as *V. Thapsus* growing by its side, so thoroughly protected by an abundance of epidermal hairs. It is not difficult to see that the woolly coating may be advantageous to young leaves, just emerging from the bud; but it is extremely difficult to find any advantage in the few simple and stellate hairs scattered over the leaves of *Lepidium* and *Capsella*.

Stomata

In over two-thirds of all the plants studied the stomata were found to be more abundant on stem than on rosette leaves. Sometimes this difference in number is only slight, but sometimes, as in *Mitella diphylla*, *Lepidium virginicum*, *Monarda punctata*, *Aquilegia canadensis*, *Campanula rotundifolia*, *Capsella Bursa-pastoris*, and *Geum album*, this difference is considerable. Stomata are also most abundant on the lower side of the leaf. This is true of about 80 per cent of all the plants studied. This difference is most pronounced in leaves that have their upper and lower sides well developed, such as the broad mesophytic rosette leaves. Narrow, xerophytic stem leaves, such as have both sides almost equally exposed to light and air, have approximately the same number of stomata on both sides. The more xerophytic the leaves, the greater are the number of stomata as compared with the corresponding mesophytic leaves. As a rule, the size of stomata is correlated with the number. The larger the number of stomata on a given leaf surface the smaller they are. This was found to be true in over 60 per cent of the specimens compared. Broad mesophytic rosette leaves have fewer but larger stomata on a given surface than the corresponding narrower, more xerophytic stem leaves. In these there is a larger number of stomata per unit surface, but the stomata are decidedly smaller in size.

There also seems to be a correlation between the number and size of stomata, and the size of epidermal cells. The broad rosette leaves have, as a rule, larger epidermal cells. With these larger cells are associated fewer but larger stomata.

Anterior-posterior orientation of stomata is noticeable in the stem leaves of *Campanula rotundifolia*, *Linaria canadensis*, *Arabis*

lyrata, *A. brachycarpa*, *A. laevigata*, and *Satureja glabra;* and in both stem and rosette leaves of *Artemisia caudata* and *Lechea villosa*. All these leaves are linear or oblong. Not all linear or oblong leaves have their stomata longitudinally oriented, but such orientation is characteristic of linear and oblong leaves, especially if the epidermal cells are longitudinally elongated.

The stomata of the species investigated are not sunken below the surface in either stem or rosette leaves, except in the sand dune xerophytes, *Artemisia canadensis* and *A. caudata*, where they are depressed about half the thickness of the epidermis. In a few instances the stomata seemed even to be elevated slightly above the surface. In *Mitella diphylla*, *Leonurus Cardiaca*, *Aquilegia canadensis*, and *Chelidonium majus*, the stomata are confined to the ventral surface of the leaf.

Rosette stomata are not only larger but also more elongated than stem stomata. Stem stomata are not only smaller but also more nearly round than rosette stomata. Perhaps the number of stomata ought to be correlated with the mass of the chlorenchyma. The smaller number of stomata in the broad, thin (frequently thicker than stem leaves), mesophytic rosette leaves, when compared with the smaller mass of chlorenchyma to be aerated, may be relatively as abundant as the larger number per unit surface in the long, narrow, thick xerophytic stem leaves, where a larger mass of chlorenchyma must be aerated through a given surface area; that is, the number of stomata is correlated with the amount of chlorenchyma to be aerated, and not with the mere surface area of the leaf. The number of stomata also seems to be correlated with the thickness of the cuticle and cutinized outer wall of the epidermis. The greater the thickness, the less is the possibility of gases passing through, and the greater is the need for stomata. It is probably for these two reasons, the greater mass of chlorenchyma per leaf surface and the greater thickness of the cuticle and cutinized outer wall of the epidermal cells, that xerophytic leaves have an increased number of stomata in a given surface area. The relatively thinner and frequently more shaded rosette leaves are broader and have a thinner cuticle, a thinner outer epidermal wall, and a greater development of air

lacunae. Such leaves need fewer and are provided with a smaller number of stomata. Stomata are not needed for transpiration, since transpiration is believed to be a necessary evil. It seems strange, therefore, that in xerophytic leaves, where there is effected the greatest protection against the loss of water by the development of a thick cuticle and a thick outer epidermal wall, there should be the development of a large number of stomata, thus facilitating the loss of water from the plant through stomatal transpiration.

In leaves whose outer epidermal wall and cuticle are thin, there is less need of stomata to facilitate exchange of gases in photosynthesis and respiration, since under such circumstances considerable interchange of gases can take place through the epidermis. There is no doubt that mesophytic rosette leaves with a reduced number of stomata have an ample supply of stomata to meet their needs. Moreover, rosette leaves are close to the soil and are therefore more advantageously situated for the intake of carbon dioxide than are stem leaves. In stem leaves the pressure of CO_2 cannot accumulate beyond 0.0003 A, or about 0.22 mm. Hg, since above this pressure it diffuses outward. But in rosette leaves close to the ground, where the exhalation of CO_2 from the soil often increases the CO_2 to 10 or more times the normal amount, a much higher pressure of CO_2 may accumulate. This increased amount of CO_2 in rosette leaves is available for carbohydrate synthesis in all cases where the leaves are not too much shaded. But since plants under normal conditions receive much more energy of sunlight (about 4 or 5 times as much) than is necessary to synthesize the small amount of available CO_2, rosette leaves are most advantageously situated for photosynthesis in spite of the reduced number of stomata and the diminished amount of light. These facts have an important bearing upon the development of chlorenchyma and air spaces in rosette leaves.

Epidermal cells

In monocotyledonous plants the epidermal cells are usually elongated. In dicotyledonous plants they are generally elongated along the ribs and larger veins, but elsewhere they may be polygonal and nearly isodiametric in outline, or entirely irregular. The

shape of the leaf, to a certain extent, determines the shape of the epidermal cells. In narrow and elongated, or linear, leaves, such as those of the stems of *Arabis brachycarpa*, *A. lyrata*, *Linaria villosa*, and *Artemisia caudata*, the epidermal cells also are elongated or linear. In such elongated or linear cells the lateral walls are quite regular. The upper epidermal cells, however, are usually more regular than the lower, except in such stem or rosette leaves as are almost equally exposed to light. Such leaves have both surfaces almost equally exposed to desiccating influences, hence the shape and size of the epidermal cells on both sides of the leaf are practically the same. This is very apparent in such xerophytic stem leaves as those of *Linaria villosa*, *Arabis lyrata*, *A. brachycarpa*, *A. laevigata*, and *Campanula rotundifolia*.

The shape and size of epidermal cells vary greatly, not only in different species and in individuals of the same species, but even in stem and rosette leaves of the same individual. There may even occur considerable variation in different parts of the same leaf. Thus in *Leonurus Cardiaca* the sinuosity of the lateral walls increases slightly from the lower to the upper stem leaves. In *Geum album* the sinuosity seems to increase from the upper to the lower rosette leaves. In *Lepidium virginicum* the sinuosity is practically the same from the upper stem leaves to the lowest rosette leaves. However, the sinuosity in the lower epidermis, in the case of *Lepidium*, is greater than in the upper epidermis. The lateral walls of the lower epidermal cells are, as a rule, more sinuous than those of the upper epidermis, and in the majority of instances (70 per cent) the sinuosity is greater in rosette than in stem leaves. Sinuosity of the lateral wall culminates under the most mesophytic conditions. Increased transpiration tends to produce relatively straight lateral walls. Hence we find the epidermal walls of the stem leaves less sinuous than those of rosette leaves, and those of the upper surface of both stem and rosette leaves less sinuous than those of the lower surface, since stem leaves are more xerophytic than rosette leaves, and the upper side of leaves more xerophytic than the lower side. Sinuosity of lateral epidermal walls is not known to be of special significance to plants. It may add a little to the strength of the epidermis and afford a larger diffusion surface

for substances passing from cell to cell. No chloroplasts are present in epidermal cells except in guard cells, and, to a slight extent, in winter leaves of *Leonurus Cardiaca*.

As to size, the upper epidermal cells are larger than the lower, and, with few exceptions, the epidermal cells of rosette leaves are larger than those of stem leaves. In 80 per cent of all observations made the epidermal cells of rosette leaves were found to be larger than those of stem leaves. The size of epidermal cells is somewhat correlated with the size of leaves, the larger leaves having the larger epidermal cells; but there are so many exceptions to this that such a general statement is not warranted.

The vertical diameter of epidermal cells is greater, as a rule, in rosette than in stem leaves (true of 80 per cent of cases), in the upper than in the lower epidermis, and usually increases from the apex toward the base of the leaf. In the middle rosette leaves the maximum diameter is usually found in the middle of the leaf. In *Capsella* there is a gradual increase from the upper stem to the lowest rosette leaves. As a rule, the maximum diameter is attained in both the middle stem and rosette leaves.

Blade, epidermal wall, and cuticle

The blade decreases in thickness from the apex to the base of the leaf. It also decreases from the upper to the basal leaves. This is less apparent in middle leaves, where the leaf sometimes increases in thickness from apex to base, or where the maximum thickness of the blade occurs in the middle of the leaf. Those leaves or parts of leaves most shaded are usually thinnest. Rosette leaves are thicker than stem leaves, owing to a greater development of spongy parenchyma. This is true more particularly of the middle and basal stem and rosette leaves. The upper stem leaves, especially the apical portions of those leaves, are frequently thicker than the corresponding portions of rosette leaves. The blade, in most instances, also appears thicker than the blades of stem leaves. Notable exceptions are *Arabis lyrata*, *A. laevigata*, *Linaria canadensis*, *Leonurus Cardiaca*, *Campanula rotundifolia*, and *Monarda punctata*. All these species, except *Leonurus Cardiaca*, have either linear or oblong lanceolate stem leaves, while the basal leaves

are broad and thin. These are plants that have almost a typical xerophytic shoot and a mesophytic rosette.

The outer epidermal wall is decidedly thicker in stem than in rosette leaves. In each of the 3 types considered, *Lepidium virginicum*, *Capsella Bursa-pastoris*, and *Chrysanthemum Leucanthemum*, the stem leaves are borne considerably above the ground and rather widely separated from each other, thus exposing them freely to air, sunlight, and desiccating winds. The rosette leaves, on the other hand, are close to the ground and considerably shaded; hence we should naturally expect this difference in thickness of epidermal cell walls. There is a slight tendency for the wall to diminish in thickness from the apex to the base of the leaf. The maximum thickness is usually reached in middle stem and apical rosette leaves, while the maximum thinness is probably to be found in the lowest rosette leaves. The outer epidermal wall on the upper surface of the stem leaves is but slightly thicker than that of the lower, especially in those upper stem leaves that grow obliquely upward so as to expose both surfaces almost equally. In the lower stem and rosette leaves this difference is much greater, the epidermal wall on the lower side being considerably thinner. The thickness of the cuticle varies with the thickness of the outer epidermal wall, the thickest wall having the thickest cuticle. The cuticle of the stem leaves of the types treated is decidedly thicker than that in the rosette leaves. It is thicker on the upper than on the lower surface of the leaf, except in the upper stem leaves, where both surfaces are about equally exposed. Here the lower cuticle is almost as well developed as the upper. The greatest decrease in thickness of cuticle is observable in the basal rosette leaves.

In interpreting the facts set forth it must be borne in mind that only middle stem leaves are compared with middle rosette leaves, and that whatever conclusions may be deduced must rest upon this comparison. Most plants have their rosettes better protected than their shoots. In 83 per cent of 30 plants observed, the cuticle is thicker in rosette than in stem leaves. In at least 75 per cent of the number the epidermal wall is also thicker in rosette than in stem leaves. Thus it seems that when the effective means of

protection of the middle stem leaves and the middle rosette leaves are compared, the preponderance of protection is in favor of the rosette leaves. However, it must be borne in mind that the difference in thickness of wall and cuticle in a number of instances is so slight as to be almost negligible. Moreover, in notable instances the stem leaves have a decidedly thicker wall and cuticle. This is true of *Chrysanthemum Leucanthemum*, *Capsella Bursa-pastoris*, *Artemisia caudata*, *Satureja glabra*, *Scutellaria parvula*, and others. *Chrysanthemum* has broad, spatulate rosette leaves on long slender petioles, while the stem leaves are oblong or oblanceolate, and have a decidedly xerophytic form and structure. The stem leaves of *Lepidium*, *Capsella*, *Satureja*, and, to a certain extent, *Scutellaria*, in like manner have a decidedly xerophytic form and structure as compared with their corresponding rosette leaves. *Artemisia* is one of those sand dune xerophytes whose stem and rosette leaves are finely dissected and almost equally exposed, and hence almost equally xerophytic in form and structure. In such mesoxerophytes as *Verbascum Thapsus*, whose leaves are thoroughly protected by a woolly coat of branching multicellular hairs, the difference in protection of stem and rosette leaves is also slight. Some plants, therefore, seem to have xerophytic shoots and mesophytic rosettes; others show a tendency to xerophytic rosettes and mesophytic shoots; while in still others the distinction is not evident.

Chlorenchyma

The apical, middle, and basal stem and rosette leaves of certain plants were studied with a view to determining the similarities and differences of the chlorenchyma of the corresponding regions of the stem and rosette leaves of the same plant. For example, an apical stem leaf and an apical rosette leaf would be selected for comparative study. Sections through the apical region of the stem leaf were then studied and the results compared with those obtained from a similar study of corresponding sections of the rosette leaf. Sections through the middle and basal regions of the leaves were similarly studied and compared. After the apical leaves were thus studied, the middle stem and middle rosette leaves, as well as the basal stem and basal rosette leaves, were similarly

studied. The thickness of the leaf, the thickness of the palisade parenchyma, the thickness of the spongy parenchyma, the number of the palisade layers of cells, and the average size of the cells of each layer, together with the size, shape, and arrangement of the cells of the spongy parenchyma, were the leading points of observation in this comparative study. All measurements are expressed in microns, and were made approximately 800 μ from the midrib of the leaf. For want of space the tabulated results cannot be given; a general summary in each case must suffice.

LEPIDIUM VIRGINICUM.—In the upper stem leaves the palisade parenchyma is almost equally developed in both the upper and lower side of the leaf. This may be due to the fact that the leaves stand at a very acute angle to the stem and are almost equally illuminated. In the middle stem leaves a lower palisade tissue is found only in the apical region of the leaf. No lower palisade layers are found in the lower stem leaves or in any of the rosette leaves. The palisade layers of the upper stem leaves are quite compact. The cells reach a maximum length in the middle stem leaves. In the basal stem leaves the cells become larger and more rounded, the layers are less closely packed and less definitely organized. The palisade cells of the rosette leaves are larger, having a decidedly greater diameter, and on the whole are less compactly arranged than in stem leaves. The upper and middle stem leaves have the thickest outer epidermal wall and cuticle. This is also true of the upper rosette leaves when compared with the lower. The difference, however, between the thickness of the epidermal wall and cuticle of the apical and basal leaves is much greater in rosette than in stem leaves.

CAPSELLA BURSA-PASTORIS.—The outer epidermal wall of stem leaves is thicker in the upper than in the basal leaves, attaining a maximum in the middle leaves. The cuticle is proportionally thickest in the upper leaves and thinnest in the proximal part of the basal leaves. Similar conditions obtain in the rosette leaves, except that the contrast between apical and basal cells is less pronounced. Palisade tissue is best developed in both upper stem and upper rosette leaves. Palisade cells are slightly longer and decidedly thicker in rosette than in stem leaves. The cells of the

spongy parenchyma are decidedly more irregular in rosette leaves, and the tissue contains a maximum of air spaces. Palisade tissue is least developed in basal stem and rosette leaves, as well as in the basal region of the leaves themselves.

CHRYSANTHEMUM LEUCANTHEMUM.—The outer epidermal wall and cuticle of the upper and middle stem leaves are very much alike in thickness, but both are decidedly thicker than the corresponding epidermal wall and cuticle of the basal stem leaves, the latter being only about one-half as thick. Rosette leaves do not differ much from each other in the thickness of epidermal wall and cuticle, but the maximum thickness may probably be found in the middle leaf. Rosette leaves, as a whole, have a thinner epidermal wall and cuticle than stem leaves, being only one-half to two-thirds as thick. The palisade tissue is better developed, as a whole, in stem than in rosette leaves, and decidedly better developed in both stem and rosette leaves in apical and middle leaves than in basal leaves. The spongy parenchyma is slightly better developed in rosette leaves and in both kinds of basal leaves. Here is found also the maximum development of air spaces.

OENOTHERA BIENNIS.—The stem leaves are thickest in the apical region and gradually become thinner toward the base. There is also a gradual increase in thickness from the apical to the basal stem leaves. The upper rosette leaves are thickest in the apical region and become thin toward the base of the leaf. In the middle and lower rosette leaves the greatest thickness is found in the middle region. From this region they gradually become thinner toward both the apex and base of the leaf.

The spongy parenchyma in stem leaves gradually diminishes from the apical to the basal region of the leaf, but there is a gradual increase in amount from the apical to the basal leaves. In the upper rosette leaves the spongy parenchyma also gradually decreases from the apex of the leaf to the base. In the middle and lower rosette leaves, however, the greatest percentage of spongy tissue is found in the apical and basal regions. In stem leaves the palisade tissue is most developed in the apical region and least in the basal region. The maximum development is probably found

in the apical and middle regions of the basal leaves. The palisade cells of rosette leaves are decidedly broader or thicker than those in stem leaves, but are relatively slightly longer. The maximum development is found in the apical and middle regions of the leaf, or in those parts of the leaves having the greatest exposure to light and other desiccating influences.

The largest epidermal cells are found in the middle region of both stem and rosette leaves. It is also in the middle of leaves that both upper and lower epidermal cells have the greatest vertical diameter. The outer epidermal wall and cuticle of stem leaves are thickest in the apical leaves, and gradually become thinner toward the basal leaves. In the upper stem leaves the outer wall and cuticle diminish from the apical to the basal region. In the middle and basal stem leaves there is less difference, and in the lowest leaves there is practically no difference in thickness of the epidermal wall and cuticle in different regions. In the upper stem leaves there is not much difference in the thickness of the epidermal wall and cuticle of the upper and lower sides of the leaf; but in the lower stem leaves the thickness is decidedly greater in the upper than in the lower epidermis. The greatest difference in thickness is found in the lowest leaves.

In rosette leaves the situation in thickness of epidermal wall and cuticle is similar to that found in stem leaves. In the upper rosette leaves, however, there is a greater difference in thickness of wall and cuticle between the apical and basal regions of the leaf. The hairs on both stem and rosette leaves are longest and most abundant on the midrib and have larger veins than elsewhere. The hairs are most abundant on the upper stem leaves and gradually diminish in number and size to the basal leaves, where they are quite small (except on veins) and only half or even less than half, as abundant. On the upper leaves they are longer and more abundant on the lower than on the upper surface, and increase in length and abundance from the apex to the base. On the middle stem leaves they are similar in size and abundance on both sides of the leaf, but slightly decrease in number from apex to base. On the basal leaves the hairs are considerably reduced in size, but otherwise the situation is similar to that found in middle stem

leaves. On rosette leaves the hairs are slightly more abundant on the upper than on the lower surface, and gradually diminish in size and number toward the basal leaves. On the lower side of the basal leaves there are very few hairs except along the margin, where they are long and abundant. The chlorenchyma contains an abundance of needle-shaped crystals of calcium oxalate, arranged in bundles (raphides). These raphides are slightly more abundant in rosette than in stem leaves.

VERBASCUM BLATTARIA.—In this species the palisade tissue is best developed in the floral leaflets and in the upper stem leaves. Here the layers are well organized and compact, and the cells reach their maximum length. In the basal stem leaves the palisade cells vary considerably in length, some being quite long, while others are quite short. Moreover, the layers are poorly organized. In the middle and upper stem leaves 3 layers are well organized, a fourth layer being only partly organized. In the basal leaves there is no trace of a fourth layer. The thickness, or transverse diameter of the palisade cells, also increases appreciably from the upper to the lowest stem-leaves. In rosette leaves there is a gradual increase in the size of palisade cells from the upper to the basal leaves. In the latter the palisade tissue is poorly developed, the cells being very irregularly and loosely arranged, and scantily supplied with chloroplasts.

With the exception of a few hairs on the ribs of rosette leaves and lowest stem leaves, this plant is devoid of hairs. The basal stem leaves and rosette leaves have the largest epidermal cells, which also have the largest vertical diameter. The upper epidermal cells of both stem and rosette leaves always have a decidedly greater vertical diameter than the cells of the lower epidermis.

The floral leaflets and upper stem leaves have the thickest outer epidermal wall and cuticle. In these leaves there is very little difference between the upper and lower epidermis. In the upper rosette leaves we also find a thicker epidermal wall and cuticle, but the difference is less pronounced than in stem leaves.

A summary of the comparative study of the upper, middle, and lower stem leaves and the corresponding upper, middle, and lower rosette leaves, based upon the 5 species just considered,

and in addition *Leonurus Cardiaca* and *Verbascum Thapsus*, is as follows.

In general the lowest stem and rosette leaves, as well as the basal part of all leaves, are most protected and most shaded, and therefore have the most mesophytic structure. The leaves are thinnest; the outer epidermal wall and cuticle are thinnest; the palisade parenchyma is developed most poorly; and spongy parenchyma, containing a maximum of air spaces and a minimum of chloroplasts, is developed most highly.

The upper stem leaves are relatively xerophytic in structure. This is especially true of the apical region of these leaves. We frequently find the maximum thickness of leaf, maximum thickness of epidermal wall and cuticle, and a maximum development of palisade tissue, which in many instances develops almost equally on both sides of the leaf. The middle and lower stem leaves are almost invariably thinner than the corresponding rosette leaves. The spongy parenchyma is better developed in rosette than in stem leaves. This was true of 75 per cent of all sections studied.

The palisade parenchyma in stem leaves is better organized, more compact, and the cells relatively longer and narrower as compared with the thickness of the leaf. In rosette leaves the layers of palisade tissue are frequently less perfectly organized, less compact, and the cells larger. Palisade cells of rosette leaves are decidedly broader and usually longer than those of stem leaves; but the amount of palisade tissue and the length of the cells, when compared with the average thickness of the leaves, are less in rosette than in stem leaves. The absolute length of palisade cells in the first layer is greater in rosette leaves than in corresponding stem leaves in 70 per cent, in the second layer in 55 per cent, and in the third layer in 28 per cent of all sections studied. In 30 per cent of all stem sections studied the second palisade layer was not developed. The same was found to be the case in 29 per cent of rosette sections studied. Likewise, the third palisade layer was not developed in 81 per cent of all stem sections studied, or in 66 per cent of all rosette sections studied. The number of sections considered in each case was the same (75 stem and 75 rosette sections). With the exception of the upper stem leaves, where the

upper and lower epidermis frequently have an outer wall of approximately equal thickness. the upper epidermis has a thicker wall than the lower. In 93 per cent of the cases the outer epidermal wall and cuticle of stem leaves were found to be thicker in stem than in rosette leaves. The thickest epidermal walls are usually found in the outer two-thirds of upper stem leaves. On the other hand, rosette leaves have epidermal cells with the largest vertical diameter and contain a maximum of air spaces.

Lepidium virginicum and *Capsella Bursa-pastoris* produce both summer and winter rosettes. When these rosettes are compared, it is found that summer rosettes have slightly thicker leaves (thinner in *Capsella*), a thicker cuticle, and a thicker outer epidermal wall. The palisade parenchyma also is better developed. There are frequently more layers, and the cells are longer and narrower. These differences are most pronounced in *Lepidium*.

SUMMARY ON CHLORENCHYMA.—Typical xerophytic leaves have a relatively compact and well developed palisade tissue; also a relatively small amount of spongy parenchyma with small air spaces. The mechanical tissue is usually also better developed than in mesophytic and shade leaves. Since rosette leaves are usually broad, close to the ground, frequently more or less shaded, and therefore in most respects better protected than stem leaves, it should not be surprising if the former were found to be more mesophytic than the latter. That this seems to be true, at least of the forms studied, is shown by the following deductions.

1. Rosette leaves, as a rule, have a greater amount of chlorenchyma than stem leaves. This is true of at least 80 per cent of all plants studied.

2. Rosette leaves have a greater amount of spongy parenchyma than stem leaves, although the percentage of the chlorenchyma is slightly greater in the latter than in the former.

3. The percentage of air spaces in both palisade and spongy parenchyma is also greater in rosette than in stem leaves. This is true of about 86 per cent of all plants studied. In a considerable number of instances, however, the differences are slight.

4. The number of palisade layers is much the same in both kinds of leaves, but the average length of palisade cells, in at least

80 per cent of the types studied, is greater in rosette than in stem leaves. This is correlated perhaps with the greater thickness of the chlorenchyma in the former. The thickness of palisade cells, in at least 90 per cent of all cases, is also greater in rosette than in stem leaves.

5. The average size of spongy parenchyma cells is also greater in rosette than in stem leaves. This is true of about 90 per cent of all plants studied.

6. Sclerenchyma tissue seems to be about equally well developed in ribs and veins of both kinds of leaves. The conductive tubes in veins of approximately equal size have a slightly larger lumen and a wall slightly thicker in rosette than in stem leaves. The conductive system of rosette leaves is better developed in rosette than in stem leaves, although this rule is not without exceptions.

On the whole, therefore, it may be said that, so far as the structure of chlorenchyma is concerned, stem leaves are more xerophytic in structure than rosette leaves, although the latter appear to be more xerophytic so far as the greater thickness of epidermal wall and cuticle are concerned. In some instances the xerophytic character of stem leaves, as compared with the rosette leaves of the same plant, is so pronounced as to be easily detected with the naked eye.

Conclusions

1. Hairs are most abundant in the upper stem leaves and decrease to the basal leaves; they are also most abundant in the upper rosette leaves and decrease to the basal leaves. In general, however, the stem leaves are more hairy than the rosette leaves.

2. Stomata are usually smaller, more nearly round, and more abundant, per unit area, on stem than on rosette leaves.

3. As a rule, the epidermal cells of rosette leaves are larger than those of stem leaves and have more sinuous lateral walls. The shape of the cells is usually correlated with the shape of the leaf.

4. The blade of rosette leaves is thicker than that of stem leaves, chiefly owing to a greater development of spongy parenchyma. This is not true, however, of stem leaves that are long,

narrow, and of a decidedly xerophytic form and structure as compared with rosette leaves.

5. The outer epidermal wall of rosette leaves is thicker, as a rule, than in stem leaves. The maximum thickness occurs in middle stem and apical rosette leaves. The thickness of the cuticle varies with the thickness of the epidermal wall, the thickest walls having the thickest cuticle. Rosette leaves in the large majority of instances have the thickest cuticle. The preponderance of epidermal protection is in favor of rosette leaves. In stem leaves of xerophytic form the preponderance of epidermal protection is in favor of stem leaves.

6. In a comparison of the different stem and rosette leaves of the same plant it is obvious that the lowest stem and lowest rosette leaves, as well as the basal part of all leaves, have the thinnest epidermal wall, thinnest cuticle, the most poorly developed palisade tissue, the maximum development of spongy tissue and air spaces, and the minimum development of chloroplasts. The upper stem leaves are relatively xerophytic in structure, especially in the apical region of these leaves. The middle and lower stem leaves are usually thinner than the corresponding rosette leaves. The palisade parenchyma in stem leaves usually is better organized, more compact, and the cells relatively longer and narrower, as compared with the thickness of the leaf, than in rosette leaves. The thickness of palisade cells of rosette leaves is greater, in most cases, than in stem leaves. This is also true of the absolute length in the great majority of instances.

7. When the chlorenchyma in middle stem and middle rosette leaves is compared we may conclude: (1) that rosette leaves, in most cases, have a greater amount of chlorenchyma than stem leaves (this is especially true of spongy parenchyma); (2) that in most cases rosette leaves also have more air spaces than stem leaves; (3) that there is little difference in the number of palisade layers in the two kinds of leaves, but in most cases the absolute size of the palisade cells (length and thickness) is greater in rosette than in stem leaves; (4) that the average size of cells of the spongy parenchyma is also greater in rosette than in stem leaves; (5) that sclerenchyma tissue is about equally developed in both kinds of

leaves, but the conductive tissue is slightly better developed in rosette than in stem leaves.

On the whole, typical rosette leaves, where there is considerable shading and protection, are decidedly more mesophytic than stem leaves. In winter leaves on stolons or runners there is a tendency toward greater xerophytism than in stem leaves, but on the whole the rosette leaves are more mesophytic in structure than stem leaves.

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IMPERFECTION OF POLLEN AND MUTABILITY IN THE GENUS ROSA*

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(WITH PLATES IV–VI)

During the winter of 1915–1916 I made a study of all the species, of which specimens were obtainable, of the genus *Rosa*. This was done in connection with work on other genera of the family Rosaceae, notably on *Rubus* and on *Crataegus;* and it has been interesting to note that in all 3 genera there is indication of a large amount of hybridism, and that the multiplication of species is startlingly great.

From the Arnold Arboretum of Harvard University, I have been able to obtain flower buds of 32 different species of *Rosa*. Of 3 of these species I have several varieties; 5 varieties of *R. spinosissima*, 3 of *R. rugosa*, and 2 of *R. virginiana*. The buds were taken when on the point of opening, thus making sure of the maturity of the pollen. They were then preserved in alcohol until such time as it was possible to examine them.

I prepared sections of about half of the species gathered, with a view to determining how many showed sound pollen and how many showed a greater or smaller proportion of undeveloped or imperfect pollen. For this purpose the buds were first imbedded in celloidin to make sure that there would be no shrinkage of the parts. Sections were cut with the microtome, stained with Heidenhain's haematoxylin and safranin, and finally mounted in balsam.

For nearly a century it has been known that one of the most important and most easily recognized characteristics of a hybrid is imperfect pollen. DUTROCHET[1] in 1832 recognized the morphological sterility of the hybrid and pointed out that pollen abortion is a criterion for hybridism. GAERTNER,[2] in 1849, speaks of the

*Contribution from the Laboratories of Plant Morphology of Harvard University.

[1] DUTROCHET, HENRI, Sterility of hybrid plants. Gard. Mag. 8:500. 1832.

[2] GAERTNER, C. F., Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich. Stuttgart. 1849.

importance of the pollen conditions in determining the fertility of a hybrid as follows:

Die wichtigste Theil der Befruchtungstheile der Bastarde ist der Pollen. Es ist nun aber zu bemerken, dass ein vollkommen normal gebildeter Pollen sein Ovarium nicht absolut zu befruchten vermag, weil manche mit wirklich potentem Pollen bestäubte Blumen nicht selten doch abortiren und unbefruchtet abfallen: obgleich in der Regel von dem Vorhandensein eines vollkommenen Pollens bei den reinen Arten auf die Fruchtbarkeit einer Pflanze geschlossen werden darf.

Since, therefore, imperfect pollen is a well known characteristic of hybrids, and one of the easiest means of identifying them, it is from an examination of the pollen of the species of *Rosa* that their probable genetical status can be determined most easily. The thin sections through the anthers, when examined microscopically, give one a remarkably clear view of the pollen grains in all positions in anthers in all parts of the different buds.

GAERTNER is again in harmony with our modern ideas in his observations concerning the difference between perfect and imperfect pollen grains, or, as he calls them, fertile and infertile; for even a hybrid may have the means, however imperfectly developed, of reproducing its kind. GAERTNER states as follows:

Die Gestalt und Grösse der Körner des Pollens der Bastarde in der nämlichen Anthere ist weit mehr verschieden, als man es nach FRITZSCHE und H. V. MOHL in den der reinen Arten zuweilen antrifft.

In den Antheren aller fruchtbaren Bastarde, befinden sich kleinere und grössere Körner mit einander vermischt in verschiedenen Verhältnissen zum Theil äusserst kleine von verschiedenen Graden der Unförmigkeit länglichte, eingeschrumpfte, leere Bälge, ohne flüssigen Inhalt—am deutlichsten findet man dies bei solchen Individuen, welche eine geringe Fruchtbarkeit besitzen. . . . . Aus der Grösse und Qualität der Pollenkörner kann man daher in manchen Fällen mit ziemlicher Zuverlässigkeit auf die Fruchtbarkeit oder Unfruchtbarkeit eines Bastards schliessen.

Die reine Farbe bezeichnet in den meisten Fällen die Potenz des Pollens.

Die Verstäubung des Pollens der Hybriden ist wie schon bemerkt sehr mangelhaft; er vertrocknet häufig in den Antheren, wenn sich diese auch öffnen.

Der Inhalt des Pollens der Bastarde ist sehr verschieden und auch selbst bei den fruchtbaren gering, meistens fehlt er aber gänzlich und der Pollen ist dann trocken und ballt sich nicht. . . . . Wenn der Pollen seine regelmässige Gestalt und Grösse hat so enthält er gewöhnlich eine flüssige ölige Materie.

That is, normal pollen is perfect morphologically, fully formed, and having normal protoplasmic contents; while abnormal or imperfect pollen, such as often characterizes known hybrids, on the contrary, is usually shrivelled and has little or no protoplasmic contents, consequently making the grain quite impotent.

The pollen of *Rosa* is largely in the last named condition, imperfect, and therefore probably sterile to a considerable extent. Of the 32 species secured from the Arnold Arboretum, 2 show entirely perfect pollen, and in 3 others imperfectly developed grains were slightly intermingled; that is, showing only 1–10 per cent bad pollen. Seventeen show a very large percentage of imperfect grains (about 50–100); and the remaining 20 show 10–50 per cent.

This enormous degree of infertility of pollen in the genus probably accounts for much of the difficulty systematists seem to have encountered in establishing species. ENGLER and PRANTL[3] speak of the genus thus:

> Die allbekannte, von Dichtern aller Kulturvölker gepriesene Rose bildet eine scharf umgrenzte Gattung, die sich durch den Bau der Blütenachse den Sanginsorbeae und Pomoideae, durch den übrigen Blütenbau den Potentilleae durch die Tracht insbesondere der Gattung Rubus anschliesst. Sie ist fast über die ganze nördliche gemässigte Zone verbreitet, geht auch in die Gebirge der Tropen über, fehlt jedoch auf der Suedl. Halbkugel.
>
> Die Zahl der Arten kann man bei mittelweiter Fassung des Artbegriffes auf etwa 100 ausschlagen, doch sind schon allein aus Europa mehrere hundert Arten niederen Ranges beschrieben worden.

The last edition of GRAY'S *Manual* recognizes 15 species of wild roses of the eastern United States and Canada, and in the last edition of *Field, forest, and garden botany*, in which are included cultivated species and varieties, there are 24 species.[4] Nine of the wild species, so-called, of GRAY (M.), I have been able to obtain from the Arnold Arboretum, also 4 of the cultivated species. The 20 odd species remaining that I have analyzed are importations, hybrids, etc., grown specially in the Arboretum. Of the 3 divisions made of the species of *Rosa* according to the percentage of bad pollen present, I shall first take up the group in which the proportion was

[3] Die natürlichen Pflanzenfamilien (p. 46).

[4] In the following pages the *Manual* is indicated by (M.), and *Field, forest, and garden botany* by (F.F.G.).

less than 10. In this group are *R. rugosa*, *R. cinnamomea*, *R. Kelleri*, *R. pendulina*, and *R. Moyesii*.

R. rugosa (figs. 5, 13) has almost no imperfect grains as may be seen in the figures, practically all of the grains being perfectly formed and full of protoplasmic contents. Fig. 5 shows the pollen teazed out of the anthers on to a slide. Fig. 13 is a cross-section through an anther, showing the pollen grains in their normal positions in the loculus of the anther. It is worth while to note also the generous quantity of pollen in the single loculus. GRAY (F.F.G.) groups *R. rugosa* among the principal types of exotic garden roses which are "much mixed by crossing and changed by variation." The reason, doubtless, for the purity of *R. rugosa* as compared, for instance, with *R. rubiginosa* (fig. 6) is its geographical seclusion on the islands of Japan. The varieties of *R. rugosa* show evidence of contamination, as will be shown later.

R. cinnamomea and the 3 other species in this group (*R. Kelleri*, *R. pendulina*, and *R. Moyesii*) have not been figured. All may be found in the Arnold Arboretum. They are all practically without imperfect pollen grains. *R. pendulina* comes from the mountains of Europe, and *R. Moyesii* comes from China.

In the second and much larger group the percentage of imperfect pollen is 10–50. In this group are *R. spinosissima altaica*, *R. spinosissima* (garden variety hybrid), *R. spinosissima*, and *R. spinosissima hispida;* also *R. spinosissima paniculata* (garden variety). *R. spinosissima fulgens* (garden variety), because of its larger percentage of undeveloped grains, belongs to the third and last group. With these are *R. Harrisoni* (garden hybrid), *R. gymnocarpa*, *R. Manetti* (garden hybrid), *R. blanda*, *R. seraphini*, *R. wichuriana*, *R.* no. 306 Wilson, *R. pratincola*, *R. multiflora*, *R. davurica*, *R. acicularis*, *R. hemispherica*, and *R. ferruginea*. Of *R. rugosa alba* and *R. virginiana alba*, which properly belong in this group, I shall speak later in connection with other varieties of the same species in the third group.

R. spinosissima and its 5 varieties present some very interesting conditions. Fig. 12 is a cross-section of the typical anther of the so-called species. It is very clearly seen that about 40 per cent of the grains in the loculus are shrivelled and without protoplasmic

contents; and the contrast between these and the perfect grains is very marked.

In comparing the species *R. spinosissima* with the recognized garden hybrid, a variety of the species and called *R. spinosissima* garden variety hybrid (fig. 10), the latter shows less pollen in the loculus, but about the same percentage of shrivelled grains. *R. spinosissima paniculata*, another garden variety, has only about 10 per cent of its pollen grains undeveloped; while still a third garden variety, *R. spinosissima fulgens*, has a larger percentage than any of the group I have examined. This last, as may be seen in fig. 11, has an abundance of pollen grains in the loculus, but about 50 per cent of them appear as tiny, shrivelled cells.

The two remaining varieties of *R. spinosissima*, *R. spinosissima altaica* and *R. spinosissima hispida*, are apparently the least contaminated of the varieties. The first, a Siberian rose (fig. 8), has a considerable amount of pollen in the loculus, and only about 10 per cent of its grains are bad. The second (fig. 9) presents an almost identical situation; and this is a European variety of the same species.

The next species in the group is *R. Harrisoni*, a recognized garden hybrid. Fig. 18 shows the poorly developed pollen typical of this species, about 40 per cent of the grains being imperfect if not entirely shrivelled. GRAY (F.F.G.) described "*R. Eglanteria* L. a yellow Eglantine rose. Like a sweetbriar, but lower. Austrian briar, Persian yellow, and Harrison's yellow are forms of this." I have not been able to obtain specimens of *R. Eglanteria* L., the parent, but certainly the offspring is an excellent example of the condition of badly developed pollen usually accepted as indicating hybridism.

R. Manetti, another garden hybrid (fig. 17), presents a condition analogous to that found in *R. Harrisoni*. *R. gymnocarpa*, a northwestern North American rose, is much less contaminated than the last two, only about 20 per cent of its pollen grains being imperfect.

The remaining species of the group under discussion present conditions more or less similar to those already described. *R. blanda* has about 20 per cent bad pollen; *R. seraphini* has only about 10 per cent; *R. wichuriana* has numerous shrivelled grains;

R. no. 306 Wilson, a Chinese wild rose, shows about 15 per cent bad pollen; *R. pratincola* has about 25 per cent of its pollen grains undeveloped; *R. multiflora* has about 20 per cent bad pollen. The last is a rose native to Japan and China, and cultivated here. GRAY (F.F.G.) records it among the principal types of exotic garden roses: "*R. multiflora* Thunb. from Japan and China. Hardy in the Middle States, a double form of an old garden rose, the single form not common. Polyantha roses are offshoots of this chiefly through hybridization with *R. indica*."

R. davurica is a Siberian rose which shows more imperfection of pollen than *R. spinosissima altaica*, having 25–30 per cent of its pollen undeveloped, in contrast with 10 per cent in the other species. *R. acicularis*, another rose native to Siberia, is in a similar condition of probable contamination; this species is now wild in the Northern Hemisphere. *R. hemispherica* is a Persian yellow rose, probably like *R. Harrisoni*, an offspring of *R. Eglanteria*. I examined the variety *R. hemispherica plena*, and found the pollen in bad condition. The last of the species in the group is *R. ferruginea*, native to the mountains of central Europe, and here also the pollen was to a large extent abortive, a condition interesting when compared with that found in *R. pendulina*, likewise a native of the European mountains, but almost without bad pollen.

In the third group are those species with 50–100 per cent bad pollen. This group is not quite as large as the second group, but presents conditions even more interesting. It includes *R. kamchatica*, *R. cordifolia*, *R. rugosa plena*, *R. rugosa alba*, *R. rugosa arnoldiana*, *R. oxyodon*, *R. rubiginosa*, *R. setipoda*, *R. mollis*, *R. macrophylla*, *R. canina biserrata*, *R. arvensis*, *R. gallica*, *R. alba*, *R. damascena*, *R. virginiana plena*, and *R. virginiana alba*.

Since the conditions as they appear in the species *R. rugosa* have already been shown, I shall first take up its 3 varieties. *R. rugosa plena* has every appearance of a typical hybrid, as evidenced by a large degree of sterility in its pollen (fig. 14). It seems clear that about 90 per cent of the pollen is abnormal; and the contamination is still more marked when we compare it with *R. rugosa* (fig. 13). *R. rugosa alba* (fig. 15) is not in such bad condition as *R. rugosa plena*, for in this case only about 40 per cent of the grains are

imperfect. *R. rugosa arnoldiana*, a garden variety which is not figured, is in even worse condition than *R. rugosa plena*, having 95–100 per cent of its pollen grains shrivelled and empty.

R. kamchatica (fig. 16) shows 50–60 per cent bad pollen. In fig. 16, with the high magnification, the imperfect grains stand out very clearly in contrast to the perfect grains. *R. kamchatica* is native to northeastern Asia, while *R. cordifolia* has its habitat in western Asia and Europe. The latter has very imperfectly developed pollen. *R. oxyodon*, a native of southwestern Asia, also has a quantity of bad pollen (fig. 7). About 75 per cent of that in the loculus is made up of shrivelled, useless grains; and this is typical of the whole species.

R. rubiginosa is perhaps the best example found of the phenomena of undeveloped pollen (fig. 6). In this case it is diffiult to find the scattered perfect grains among the host of abnormalities present. The condition is particularly striking when compared with that found in *R. rugosa* (cf. fig. 6 with fig. 5). GRAY (M.) remarks in reference to this species that it is inconstant and suggests relationship to *R. canina*.

ENGLER and PRANTL (Nat. Pflanzenfam.) under the group Cynorrhodeae name several species which have been examined and put in the third group.

> Die Rosen dieser Gruppe sind durch Europa und das Westliche Asien in äusserst zahlreichen Formen verbreitet, welche die Artumgrenzung in vielen Fällen ungemein schwierig machen. *Vielfache Kreuzungen der Arten unter einander, sowie R. gallica* L., *R. alpina* L., *u. s. w. haben zur Mannigfaltigkeit der Formen wesentlich beigetragen.*[5] Als die Hauptarten, um welche sich die verwandten Species gruppieren lassen, können *R. canina* L., *R. rubiginosa* L., *R. mollis* Sm., *R. tomentosa* Sm., und *R. elymaitica* Boiss. betrachtet werden.

I have not figured *R. setipoda* and other species recorded later, but I have examined the pollen of all. *R. setipoda* is a native of Western China, and it is difficult to find a perfect pollen grain in any of its anthers (cf. *R. Moyesii*). *R. mollis* has only about 60 per cent of its pollen grains bad. *R. macrophylla*, a rose from the Himalayas, is in quite as bad a condition as *R. setipoda*. *R. canina biserrata*, a native of Europe found here in both wild and culti-

[5] The italics are the writer's.

vated forms, shows but 10 per cent of the microspores fully formed. *R. arvensis* has only 25 per cent of its pollen grains normally developed. It is often cultivated, and is mentioned by GRAY (F.F.G.) in connection with *R. sempervirens*. The latter is "an Ayrshire rose, evidently an offshoot of *R. arvensis*, a closely related species." In ENGLER and PRANTL (p. 49), under the division with "Kriechende und kletternde Arten," note the following:

R. repens Scop. (*R. arvensis* Huds.) wächst auch im westlichen Mittel-Europa wild, während die immergrüne *R. sempervirens* L., den Mittelmeerländern angehört. Von diesen beiden weiss blühenden Arten stammen die kletternden Ayrshire-Rosen welche von den Gärtnern auch mit Theerosen (*R. indica* var.) und anderen Arten gekreuzt worden sind.

R. gallica, the cabbage rose, is another interesting species, showing about the same proportion of bad pollen as *R. arvensis*. *R. alba* shows a very large percentage of abnormal grains, and is designated as a "*natural hybrid*" of Europe. *R. damascena* has about 60 per cent of pollen imperfection and is, according to GRAY (F.F.G.), "closely allied to *R. centifolia*." In connection with this species also, GRAY (F.F.G.) says "hybrid perpetual roses are largely derived from this through hybridization with forms of *R. indica* and others."

In reference to the last 3 species described, ENGLER amd PRANTL (Nat. Pflanzenfam., p. 47) furnish some interesting information.

R. gallica L., an welche sich *R. damascena* Mill., *R. alba* L., und andere vermeintliche Arten anschliessen, die noch nirgends wirklich wildwachsend nachgewiesen sind und warscheinlich nur als Kulturpfl. existiren. *R. damascena* zeigt eine Annäherung an *R. moschata* Mill., während *R. alba* den Mischlingen aus *R. gallica* und *R. canina* sehr ähnlich ist. . . . . In diesen Formenkreis, dessen Mittelpunkt *R. gallica* ist, gehören alle die edlen, meistens gefüllten Gartenrosen orientalsich-europäischen Ursprungs.

Ganz unabhängig davon ist in Ostasien ein zweiter Formenkreis von gefüllten Gartenrosen gezüchtet worden, welche man auf eine einzige Stammart, *R. indica* L. zurückführt. Neuerdings sind europäische und ostasiatische Kulturrosen vielfach gekreuzt worden. . . . . In den neueren Gartenrosen sind alle diese Arten und Varietäten mit einander verschmolzen worden. Die natürliche lange Blütezeit der *R. indica* hat sich auf manche ihrer Kreuzungsformen vererbt und hat den Anstoss zur Entstehung der lange blühenden und zweimal blühenden Gartenrosen gegeben.

Three species of this last group remain to be mentioned. *R. setigera* shows a large percentage of microsporic degeneracy. *R. virginiana plena* with about 90 per cent of its pollen bad, and *R. virginiana alba* with but 25 per cent of its pollen imperfect, are varieties of the *R. virginiana* Mill. of GRAY'S *Manual*. The latter, known sometimes as *R. lucida* Ehrh., is a dwarf wild rose found on the margins of swamps and rocky shores from Newfoundland and eastern Quebec to New York and eastern Pennsylvania.

The preceding statistics show clearly that the species of *Rosa* are in a very marked degree characterized by abnormal pollen. It is true likewise that abnormal pollen is largely sterile. Pollen sterility for nearly a hundred years has been recognized by plant breeders as a prominent characteristic of hybrids; and another well known characteristic of hybrids is their extreme variability. Since both extreme pollen sterility and variability are prominent features of hybrids, the conclusion seems inevitable that most of the so-called species of *Rosa* are in reality hybrids.

This conclusion is most interesting when viewed from an evolutionary standpoint. Are new species the result of gradual changes or sudden leaps? The answer to this depends largely upon the definition of the term species. In the lower vascular plants the conditions of spore abortion and hybridization appear to be very rare. The term species in these cases, therefore, is used to distinguish groups of plants wholly distinct from one another and probably genetically pure. JEFFREY[6] has shown by microscopical investigation that morphologically sterile pollen does not occur in plants that are monotypic, isolated geographically or through the time of flower maturity. He has likewise made a comparison of the "conditions of sporogeny found in the lower plants, the Bryophyta, Pteridophyta, and gymnosperms, which are not characterized by enormous multiplication of species, with the sporogenic features of the angiosperms in which multiplication of species has run riot." In this comparison he found that in the lower forms of Embryophyta, from the Bryophyta to the gymnosperms, "infertile spores and hybridism were conspicuous by their

[6] JEFFREY, E. C., Some fundamental morphological objections to the mutation theory of DEVRIES. Amer. Nat. **49**:5–21. *figs.* 7. 1915.

absence." Among the gymnosperms he examined Cycadales, Ginkgoales, Coniferales, and Gnetales, and found "a single species of *Abies* with evidence of abortive pollen grains of hybrid origin."

The photomicrographs of *Lycopodium complanatum* and *Pinus divaricata* (figs. 1, 2) show clearly the morphological condition typical in both genera, fertile spores uncontaminated by any abnormal, sterile grains. JEFFREY states that "the genus *Pinus* is very old and its species accordingly very distinct"; and he has not yet found "the slightest evidence of hybridization here or in other numerous and widely distributed species of conifers, other than the *Abies* mentioned above."

In the angiosperms, on the contrary, hybridism as a condition widespread in nature is commonly recognized. For example, in this country and in Europe systematic botanists agree that hybridism is extremely common as a natural condition in certain genera of the Rosaceae. BRAINERD has shown that a great many "natural hybrids" of *Rosa* and *Rubus*, occur; and JEFFREY[7] in a recent article says as follows:

> Not only are certain of the Rosaceae recognizable as hybrids on account of their transitional external features of organization, Mendelian phenomena, etc., but certain others which have not revealed themselves as hybrids in these ways are clearly such as a result of a study of their spores. . . . . Taking morphological features into account, as well as the data of the systematic botanists, there are three kinds of individuals; pure species, recognized species with pollen showing they are concealed hybrids or crypthybrids, and recognized hybrids or phenhybrids.

These 3 classes, typical of many angiospermous genera, make it difficult to determine what individuals shall form a species. In the higher vascular plants, therefore, the term species is obviously used in a very different sense from that in which it is applied to the lower vascular plants. Clearly crypthybrids should not be species in the same sense in which the name is used of *Pinus* and other morphologically normal genera. But they are generally admitted by the systematist as good species because of their relative constancy and the absence of observed intergrading types, though the morphological conditions are undoubtedly those of hybrids.

[7] JEFFREY, E. C., Spore conditions in hybrids and the mutation hypothesis of DEVRIES. BOT. GAZ. **58**:322–336. *pls. 22–25.* 1914.

Now if crypthybrids could *justly* be called true species, it might possibly be admitted that they to some extent support the mutation theory of DEVRIES. But unfortunately they are frequently, although not universally, very variable, and this variability would appear on morphological grounds to be the result of hybridization.

On the other hand, the natural hybrid or phenhybrid found in the angiosperms and resulting from a cross between distinct species, with no segregation as in Mendelian crosses, but a blending of the parent characters, may breed true to these respective characters, in which case a new and distinctive form is perpetuated, and to this the systematist may justly give a specific rank. Such forms, however, are usually characterized by a large amount of sterile pollen, unlike the true species in which the pollen is morphologically perfect. Hence the term species is used here in a sense somewhat different from that ordinarily implied.

In proportion to the extension of the term species, the number of species has grown astonishingly. This multiplication of species is probably largely due to hybridization, judging from the morphological data afforded by the Rosaceae; and generally the new "species" are crypthybrids. HOAR[8] of this laboratory has been investigating *Rubus* and has reached results corresponding to those recorded here with regard to *Rosa*. Hybridism appears to be even more rife in *Crataegus*, and the multiplication of species is likewise greater, as is shown by the result of work carried on by Miss LORA STANDISH.[9]

It is interesting to note how many of the species of the genus *Rosa* in cultivation at the Arnold Arboretum are really crypthybrids, and how many are true species and phenhybrids. Take the 3 groups as presented according to their pollen sterility. To the first group only can the term species be accurately applied, that is, in the strict sense of the word as used of species of *Pinus* and *Lycopodium;* for only in this group is the percentage of sterile pollen so negligible that the members may be considered, with some degree of probability, genetically pure.

[8] HOAR, C. S., Sterility as the result of hybridization and the condition of the pollen in *Rubus*. BOT. GAZ. **62:** 370–388. 1916.

[9] STANDISH, LORA, What is happening to the hawthorns? Jour. Heredity **7:** 266–279. 1916.

In the second group there are 3 phenhybrids and 3 garden varieties probably of hybrid origin though not so designated. The remaining 14 are crypthybrids, several of which are treated as species in standard systematic works; as for example, *R. blanda* with 20 per cent of its pollen grains abortive, and *R. rubiginosa* with pollen almost completely undeveloped.

In the third and last group I find 3 phenhybrids; one natural hybrid of known parentage, *R. alba;* two recognized hybrids, *R. rubiginosa* regarded as derived from *R. canina*, and *R. damascena* which is allied to *R. centifolia* and parent with *R. indica* of "hybrid perpetual roses"; and two garden varieties of *R. rugosa* which are also of recognized hybrid origin. The remaining 12 of this group are crypthybrids.

These crypthybrids of *Rosa* are particularly interesting in connection with the several theories of the origin of species. We know that they are common not only in the Rosaceae, but, as has been shown to be probable, also in the Onagraceae and other families of the angiosperms. Such forms, though recognized as species, obviously cannot rank with pure species in the sense in which that term is applied to gymnosperms, etc., in evolutionary discussions; for, as JEFFREY has recently stated (see footnote 6), "The conduct of such forms is conditioned more or less by their mixed blood."

In this connection it is interesting to note the conditions presented by *Oenothera Lamarckiana* and other species of the genus as described by DEVRIES and other authors. Here we have, as is the case in *Rosa*, a considerable degree of variability accompanied by a large amount of pollen sterility. Upon *Oenothera* and forms manifesting similar peculiarities DEVRIES has mainly based his mutation hypothesis.

To go back to the original question, are new species the result of gradual changes or sudden leaps? The Darwinian hypothesis, as has been pointed out, is in large measure supported by the species of *Pinus*. But, as I have shown, the term species when used of *Pinus* has an altogether different significance from that which it has when used of *Rosa;* and consequently, the problem of evolution as presented by the species of *Rosa* must be an entirely

different one. There must be careful distinctions made between the 3 classes of individuals; and the search for the true solution of the problem of the origin of species becomes thereby a matter of great complexity. As for the mutation hypothesis of DEVRIES, the morphological and systematic evidence set forth with regard to the conditions in *Rosa*, and the similar conditions brought out with regard to *Rubus*, *Crataegus*, and the Rosaceae as a whole, seem to lend it little support, since the mutability here is obviously the result of hybridization in nature.

Conclusions

1. The species of *Rosa* are characterized by a large amount of abortive pollen and also by great variability.

2. Both pollen sterility and variability have long been recognized as two main characteristics of hybrids.

3. The species of *Rosa*, therefore, are largely of hybrid origin.

4. On account of the great number of crypthybrids and phenhybrids in angiosperms, the term species has a very different meaning from that which it has when applied to the lower vascular plants and the gymnosperms.

5. The mutability of the species of *Rosa* cannot properly be used in support of the mutation hypothesis, since this phenomenon is obviously the result of hybrid contamination in nature.

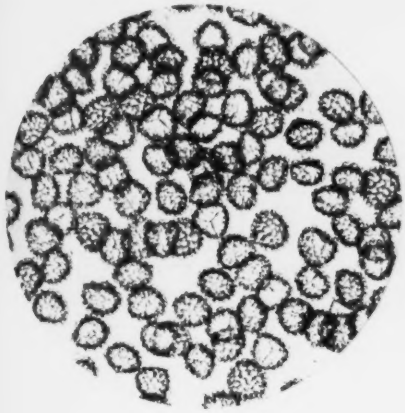
In conclusion the writer wishes to express her most sincere thanks to the Director of the Arnold Arboretum for permission to collect material; and to Professor E. C. JEFFREY for advice and assistance.

HARVARD UNIVERSITY

EXPLANATION OF PLATES IV–VI

PLATE IV

FIGS. 1–6.—Pollen.
FIG. 1.—*Lycopodium complanatum;* ×125.
FIG. 2.—*Pinus divaricata;* ×125.
FIG. 3.—*Rosa alba;* ×250.
FIG. 4.—*Rosa alba;* ×375.
FIG. 5.—*Rosa rugosa;* ×250.
FIG. 6.—*Rosa rubiginosa;* ×375.



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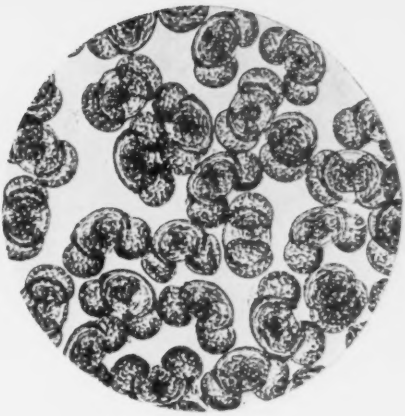

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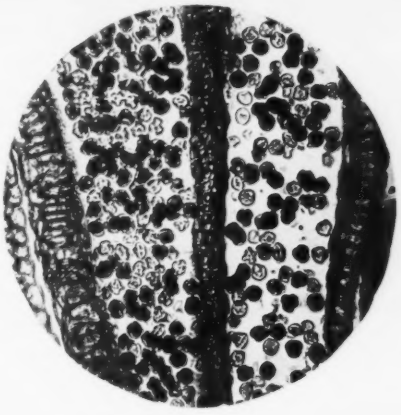
COLE on ROSA



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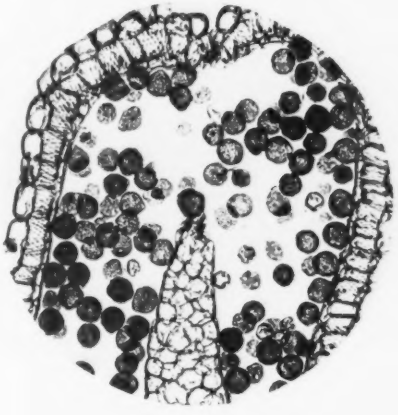

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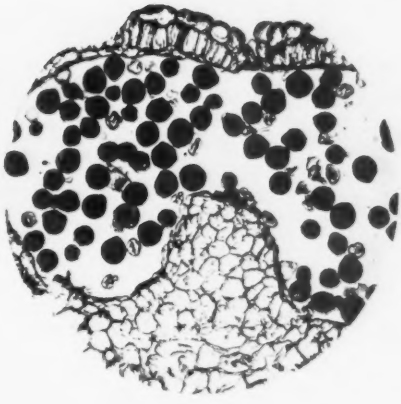

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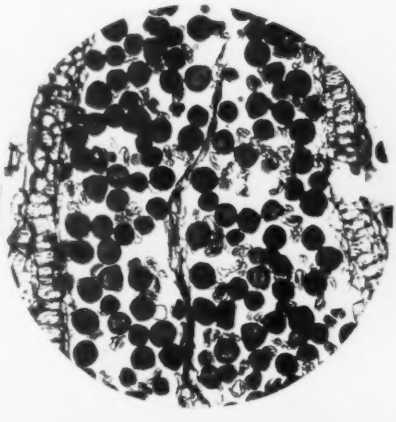

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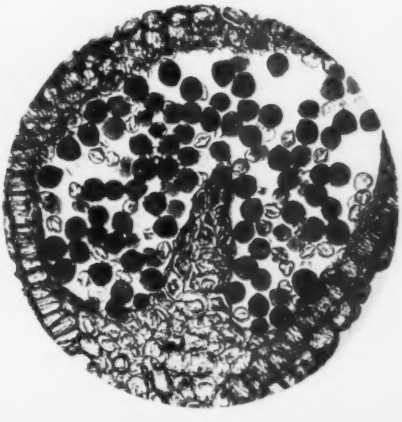

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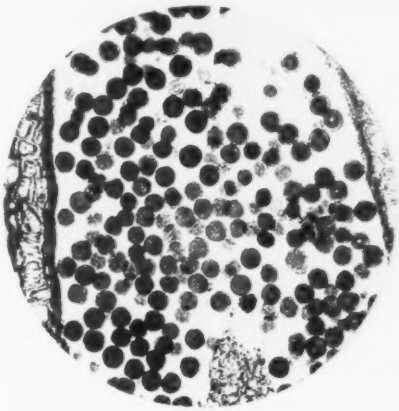
COLE on ROSA



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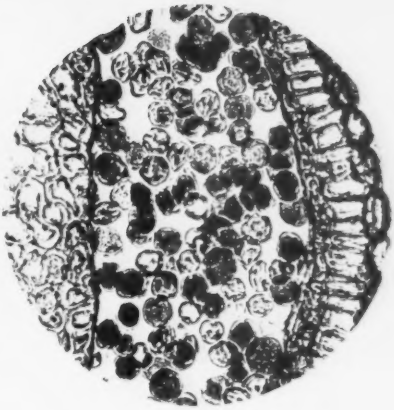

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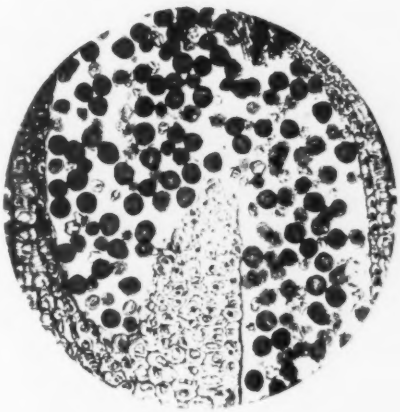

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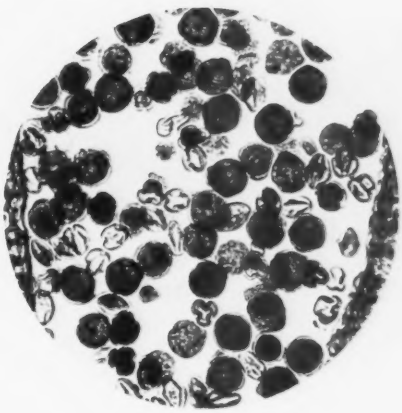

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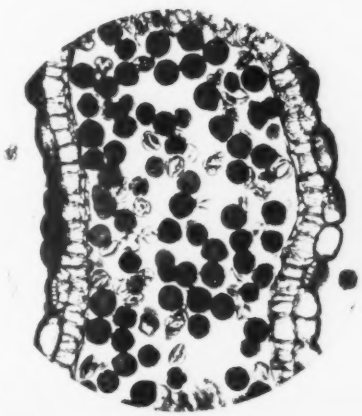

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18

COLE on ROSA

PLATE V

FIGS. 7–18.—Transverse sections of anther.
FIG. 7.—*Rosa oxyodon;* ×125.
FIG. 8.—*Rosa spinosissima altaica;* ×125.
FIG. 9.—*Rosa spinosissima hispida;* ×125.
FIG. 10.—*Rosa spinosissima* (gard. var. hyb.); ×125.
FIG. 11.—*Rosa spinosissima fulgens;* ×125.
FIG. 12.—*Rosa spinosissima;* ×125.

PLATE VI

FIG. 13.—*Rosa rugosa;* ×125.
FIG. 14.—*Rosa rugosa plena;* ×125.
FIG. 15.—*Rosa rugosa alba;* ×125.
FIG. 16.—*Rosa kamchatica;* ×250.
FIG. 17.—*Rosa Manetti;* ×125.
FIG. 18.—*Rosa Harrisoni;* ×125.

MORPHOLOGY OF KETELEERIA FORTUNEI

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 225

A. H. HUTCHINSON

(WITH PLATES VII AND VIII AND THREE FIGURES)

Since its discovery by FORTUNE, *Keteleeria* has aroused interest as an endemic Chinese conifer. It was found first near the temple of Foo Chow Foo, and reports of recent explorers locate it near ancient shrines. Whether *Keteleeria*, as seems most probable in the case of *Ginkgo*, was a sacred tree and has been preserved by a religious order is a matter of conjecture.

Because of limited knowledge, even of the gross structure and characteristics, it is not surprising that the form now known as *Keteleeria* has been variously placed by systematists. LINDLEY named this form *Abies jezoensis*, mistaking it for a Japanese species of that name (**14**). MURRAY, in 1862, showed that the form in question differed from *Abies jezoensis* and called it *Abies Fortunei* after the original discoverer. In 1868 CARRIÈRE made a new genus *Keteleeria*, naming it after KETELEER, a Belgian horticulturist. PARLATORE placed the same form under the genus *Pinus*, as *P. Fortunei;* by BENTHAM and HOOKER it was classified with *Tsuga;* BENTHAM and MASTERS again placed it in the genus *Abies;* while by ENGLER it is described under *Abies*.

CARRIÈRE'S reasons for making a new genus were that the form in question differs from *Picea*, since it has erect cones; it cannot be included with *Abies* because the cone scales are persistent; and at the same time, in habit and general aspect it resembles *Podocarpus*. Further, PIROTTA (**14**) states that a new genus is justified because of the arrangement of the staminate strobili ("fiori maschili"). The bud of the staminate strobili is borne either in the axils of the leaves of the preceding year or at the apex of a branch. PIROTTA regards the cone clusters as true "inflorescences." Each "inflorescence" consists of a short peduncle dilated at the apex into a receptacle-like body which is invested

by scales; the lower scales are short, those above becoming increasingly longer. The "flowers" are situated on the margin of the dilated peduncle in the form of a circle or false crown, one or two "flowers" being situated near the center of the receptacle. The number of staminate cones in a cluster ranges from 6 to 10. It is rather remarkable that the other genus of Abietineae (*Pseudolarix*) which shows such an arrangement of staminate cones is also an endemic of China. PIROTTA regards this character of sufficient importance to warrant the division of Abietineae into the Euabietineae, including those forms whose staminate strobili are single (*Abies*, *Picea*, *Pseudotsuga*, *Tsuga*), and the Pseudoabietineae, including those forms whose staminate strobili are in clusters (*Keteleeria* and *Pseudolarix*).

PIROTTA (**15**) has examined also the anatomical structure of the root, stem, and leaves. The root is characterized by a primary axial resin canal, by secondary canals arranged irregularly in the secondary wood, and by the presence of resin-bearing "idioblasts" in the secondary cortex. In the branches there are resin canals and mucilage-bearing "idioblasts" in the primary cortex only. The leaves are bilateral and contain 2 marginal resin canals and also mucilage "idioblasts" in the mesophyll.

The vascular anatomy has been studied also by HOLDEN (**11**), who says "*Keteleeria* has the wood structure of *Abies*. Ray tracheids are entirely absent even in such primitive structures as the first annular ring, cone-bearing branches, cone axis, and are not recalled after wounding, although there is an abundant formation of traumatic resin canals."

RADAIS (**17**) has classified conifers according to the distribution of the resin ducts ("caneau sécréteurs") in the megasporophylls. Upon this basis *Keteleeria* is placed with *Cedrus* and *Picea*, cross-sections of the sporophyll, about the middle of the seed, showing resin ducts in both inner and outer parenchyma; in *Tsuga*, *Larix*, *Pseudotsuga*, and *Abies* they are situated in the inner parenchyma; and in *Pinus*, in the outer parenchyma only. This classification, according to the admission of the author, is "surtout artificiel."

The anatomy of the staminate strobilus has been described by AASE (**1**). The general tendency in the evolution of conifers

to proceed from separate bract and scale to the fused bract and scale is noted; in the first group the bract and scale are separate almost to the base of the appendages, and both are about equally prominent. To this group belong *Keteleeria*, *Pseudotsuga*, species of *Abies*, and species of *Larix*.

MALE GAMETOPHYTE.—The multiplication of the cells in the male gametophyte follows the sequence characteristic of the Abietineae. There are 3 successive primary divisions; by the first and second the 2 polar ("prothallial") cells are cut off, the third resulting in the formation of the antheridial cell and the tube nucleus (figs. 1–5). This stage is the most advanced found in available material, and is believed to be the stage at which the pollen is shed. With respect to the development of the male gametophyte at the time of shedding, *Keteleeria* would resemble *Pinus* and might be contrasted with *Abies* and *Picea*. The appendage-like outgrowths of the exine and the inflation of the region between the exine and intine, caused by this growth, result in the production of wings, such as are characteristic of the Abietineae.

The mitoses involved in the development of the male gametophyte are similar to those described for *Abies* and *Picea* (**12,13**). In each of the first 3 mitoses the spindle fibers become oriented in such a way that they surround the polar nucleus; later they radiate from it, appearing in cross-section as tufts of fibers. This peculiarity of the mitotic figure doubtless is associated with the unequal apportionment of the cytoplasm to the resulting nuclei, an inequality which results in more favorable conditions for the more centrally placed nucleus.

In *Keteleeria* the development of the male gametophyte is not uniformly as described. Fig. 5 shows 4 nuclei medianly placed and almost equal in size. The association of such gametophytes with others whose nuclei and cells are unequal and differently placed indicates that the degree of development depends upon conditions, rather than being foreordained. When inclosed by a wall containing little cytoplasm the nucleus soon disintegrates. Fig. 4 shows 3 nuclei which are "prothallial" in nature; the third under ordinary conditions would be regarded as antheridial; in

this case the nucleus corresponding in origin to the tube nucleus has taken the central position. In the struggle the nucleus which is most centrally placed gains the ascendency, the others being crowded to the wall.

MORPHOLOGY OF THE OVULATE STROBILUS.—The anatomy of the megasporophyll has been studied by AASE (1). "In *Keteleeria Fortunei* one bundle originates near the base of the gap in the strobilus cylinder and supplies the bract. It remains undivided throughout its course. Two bundles, one from each side of the gap, supply the scale; the two bundles soon unite, forming one inverted bundle, that is, its xylem faces the xylem of bract." However, in the early stages the strands connected with the 2 ovules are separate. The evidence supports the theory that the scale with its megasporangia represents a fertile bud in the axil of the bract.

The material studied shows that at the time the pollen is shed the megasporangium has reached the mother-cell stage. There is only one megaspore mother cell and it is the fourth cell from the epidermis (fig. 9), characters which still further emphasize the relation of *Keteleeria* to the Abietineae.

SIEVE TUBES.—The sieve tubes of *Keteleeria* are large, 8–10× 200–400μ, and are well differentiated. Concerning the sieve tubes of gymnosperms, DEBARY (5) states that "the oblique terminal faces are directed toward the radial planes. Sieve plates are placed in one or two longitudinal rows over the terminal faces and the whole remainder of the radial lateral face. They form roundish spots separated by high intervening portions. These spots are coarsely latticed, while in the cavities of the coarse lattice the very delicate sieve structure is seen." The appearance as seen in a surface view only has been described, and this has led to an erroneous idea of the structure. The description given by HABERLANDT (6) and DEBARY might apply to the structures as represented in fig. 6. However, transverse and tangential sections show no thickenings or depressions in the walls of the sieve tubes. The appearance of "delicate sieve structures" described for radial sections is caused by the presence of granular inclusions in protoplasmic aggregations which are situated on either side of groups

of perforations in the sieve tube walls. The protoplasmic masses are connected by delicate strands which penetrate these perforations (figs. 7, 8).

The general tendency in the modification of sieve tubes from the lower to the higher vascular plants is toward an increasingly smaller number of sieve plates. First, there is a decrease in the number of walls upon which the plates occur. In some ferns each sieve tube wall contiguous with the wall of a similar cell bears sieve plates, while in most angiosperms they occur on the terminal walls only. Again, there is a tendency toward diminution in the number of plates on a given surface. In ferns (**5**, p. 180) there are several rows of plates, or they may be closely crowded together; in *Vitis* there are a number of elongated plates on the oblique septae; in cucurbits there is a single plate. In *Keteleeria* the occurrence is limited to the walls seen in radial sections and the oblique terminal walls. This is true of gymnosperms in so far as the records are available. The plates are arranged in a single interrupted series of groups. In this respect *Keteleeria* is much more advanced than *Encephalartos* (**5**, p. 181, *fig. 78*); the latter has plate groups closely distributed over the radial faces. Moreover, the plate groups are much less numerous on the radial faces in *Keteleeria* than on the oblique terminal faces. This is a further advance toward the condition in angiosperms. It seems probable that the investigation of other forms in this respect would give valuable evidence with reference to genetic relationships.

EMBRYO.—The embryo of *Keteleeria* is of considerable morphological interest; it throws light upon the polycotyledonous embryo of Coniferales, and also the meristem of the primary root shows characters heretofore unknown among gymnosperms (**2, 7, 8, 9, 10**). PIROTTA (**16**) has described the seedling.

In the embryo, as found in the mature seed, the following regions occur: cotyledons, leaf bud, and primary root. Beginning at the exterior, a cross-section of the root, taken near the central region (figs. 24, 25), shows the coleorhiza, the cortex, the region of meristematic cells and mucilage cells, and the central axis.

There is a cotyledonary tube which extends throughout approximately two-thirds of the length of the embryo. The cotyledons

proper are terminal upon the cotyledonary tube, and their length is about one-sixth of that of the tube. At the base the tube is in the form of a hollow cylinder (fig. 19) above; the inner surfaces become rectangular, then star-shaped in outline (figs. 16, 17); finally, the 4 cotyledonary tips become separate (fig. 16).

Occasional seedlings of *Abies* and *Pinus* have been described (**7, 8, 9, 10**) having limited cotyledonary tubes, but no such pronounced structure as occurs in *Keteleeria* has been recorded. Although the material did not show the earlier stages, it seems evident that the situation here is similar to that existing in angiosperms (**3, 4**); that cotyledons, whether several as in Coniferales, two as in dicotyledons, or one as in monocotyledons, are all similar in origin; that the cotyledonary growth is, primarily, that which results from a meristematic ring about the leaf bud, the number of cotyledons being dependent upon the number of the loci of increased growth. In *Keteleeria* the major part of cotyledonary elongation is uniform throughout the entire ring of the growth region.

With the exception of the central axis, the regions of the primary root are similar to those of other conifers; in *Keteleeria* this region is continuous throughout, while in other conifers described it is broken by the meristematic region. It is evident that such a modification in structure is due to the nature of the meristem. Since the meristem of certain conifers, including *Keteleeria*, is being described in another paper, details may be omitted here.

The differentiation of tissues as they occur in the embryo of the mature seed is advanced beyond the stage usual for conifers (**7, 8, 9, 10**). In the primary root the first cells to become differentiated are those which later become mucilage tubes (shown in black, figs. 15–27). The cells cease to divide and become vacuolate (fig. 11); the nucleus disintegrates; the cells are greatly elongated by division and growth of the surrounding cells and become mucilaginous in content. Similar cells, except that they are much shorter, are formed in the coleorhiza. The cells of the cortex become filled with food materials, generally in the form of starch (fig. 12). The cells forming a hollow meristematic cylinder about

the central axis divide in either of two planes (fig. 13). The first xylem elements, having the usual spiral thickenings of the protoxylem, become differentiated in the cotyledons; there are 4 groups of protoxylem, with 2–4 strands in each group, extending

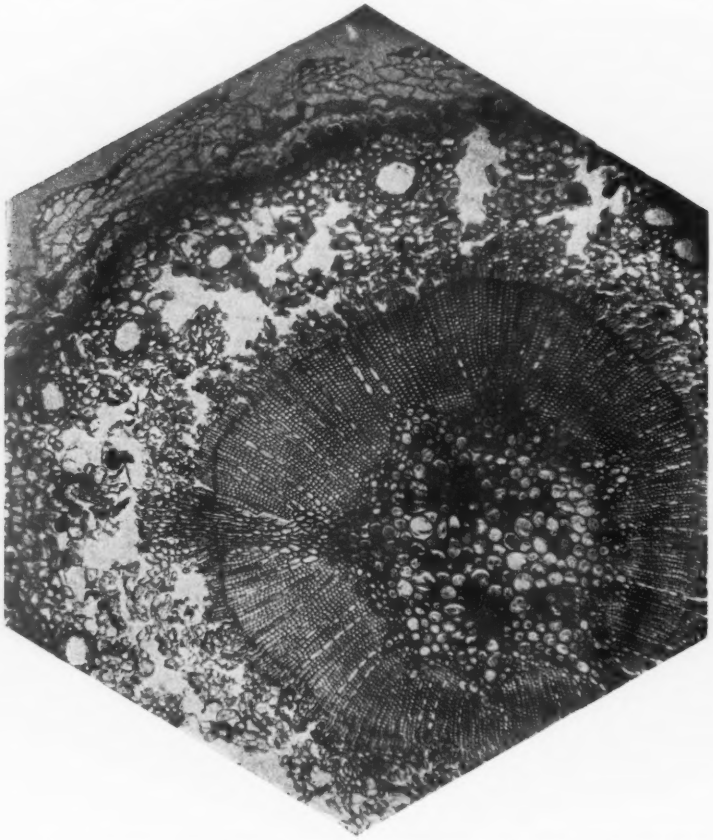

FIG. 1.—Transverse section of a branch showing epidermis, cork cambium, cortex with resin ducts, phloem, xylem, pith, and a leaf trace.

from near the tip of the cotyledon to the base of the cotyledonary tube. The protoxylem is endarch (figs. 16–20). It is significant that at this time there is no xylem present in the primary root or in the leaf bud (stem tip).

The 4 meristematic regions of the cotyledonary tube, with which the protoxylem is associated, and also the meristem of the leaf bud, connect with the hollow meristematic cylinder of the primary root. The central axis extends beyond this junction point, thereby modifying the structure generally known as the cotyledonary plate (fig. 15) (**7, 8, 9, 10**).

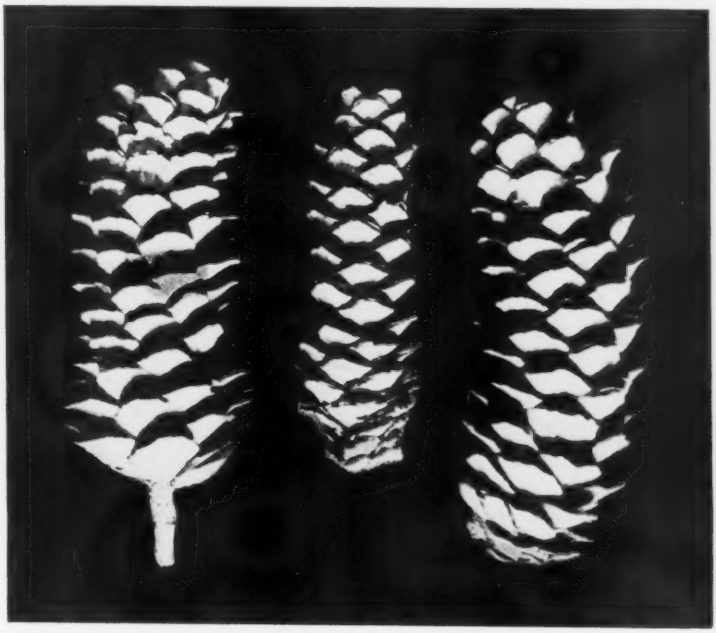

FIG. 2.—Mature ovulate cones

Summary

The following characters of the form in question warrant a genus *Keteleeria*, belonging to the Abietineae.

1. *Ovulate strobilus.*—(1) The cones are erect (text fig. 2); (2) the scales are persistent (text fig. 2); (3) the scale and bract are separate nearly to their bases (text fig. 3); (4) there is a single megaspore mother-cell (fig. 9).

2. *Staminate strobilus.*—(1) The staminate cones are borne in clusters on a fertile branch (text fig. 3); (2) there are 2 abaxial microsporangia on each sporophyll; (3) the pollen is winged (figs. 1–5).

3. *Male gametophyte.*—The pollen is shed in the 4-celled stage, consisting of 2 polar cells, the antheridial cell, and the tube nucleus (figs. 2–3).

FIG. 3.—Above, megasporophylls with scale and bract separate nearly to the base; below, fertile branches bearing groups of staminate strobili; between, 2 winged seeds.

4. *Vascular anatomy.*—(1) Resin ducts do not occur in the secondary wood except as traumatic responses (text fig. 1) (11); (2) there are no ray tracheids nor are they "recalled by wounding" (11).

5. *Embryo.*—(1) There is an extensive cotyledonary tube (figs. 15–20); (2) a central axis extends throughout the primary root (fig. 15).

6. *Leaves.*—(1) The leaves are spirally arranged on ordinary branches; (2) there are 2 very closely associated vascular strands and 2 marginal resin ducts (**15**).

7. *Sieve tubes.*—These present single interrupted rows of plate groups on the radial and oblique terminal faces. Paired protoplasmic accumulations, one on either side of each plate, are connected by strands which penetrate small perforations in the intervening walls (figs. 6–8). The sieve tubes are more numerous on the oblique terminal faces, an advance toward the angiosperm condition.

8. *Cotyledonary tube.*—This is significant in connection with the theories of the origin of polycotyledony.

The writer wishes to express his thanks to Professor J. M. COULTER and Professor C. J. CHAMBERLAIN for material provided and for advice and direction during the progress of the investigation.

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EXPLANATION OF PLATES VII AND VIII

FIGS. 1–5.—Male gametophyte; ×1630.

FIG. 1.—First polar cell and second primary mitosis.

FIGS. 2, 3.—Two polar cells, antheridial cell, and tube nucleus; in fig. 3 the wall which later cuts off the antheridial cell has not yet been formed; the radiating fibers may be noted.

FIG. 4.—Three nuclei have been crowded to the wall ("prothallial cells"); tube nucleus is central.

FIG. 5.—Four medianly placed nuclei, alike in size and structure.

FIGS. 6–8.—Sieve tubes with sieve plates; ×1630.

FIG. 6.—From a longitudinal radial section.

FIG. 7.—From a longitudinal tangential section.

FIG. 8.—From a transverse section, a cell from the pith ray being shown also.

FIG. 9.—Megasporangium showing megaspore mother-cell.

FIGS. 10–14.—Cells from different regions of the embryo.

FIG. 10.—Cells from meristem of cotyledon.

FIG. 11.—Cells becoming differentiated to form mucilage tubes.

FIG. 12.—A cortical cell.

FIG. 13.—Cells from meristem of primary root.

FIG. 14.—From protoxylem of cotyledonary tube.

FIGS. 15–27.—Semidiagrammatic drawings of the embryo; ×40.

FIG. 15.—Longitudinal median section; attached numbers indicate region from which accompanying transverse sections have been taken.

FIGS. 16–27.—Transverse sections.

FIG. 16.—Cotyledons.

FIGS. 17–20.—Cotyledonary tube, showing meristematic region and protoxylem (black).

FIG. 20.—Cotyledonary tube and leaf bud.

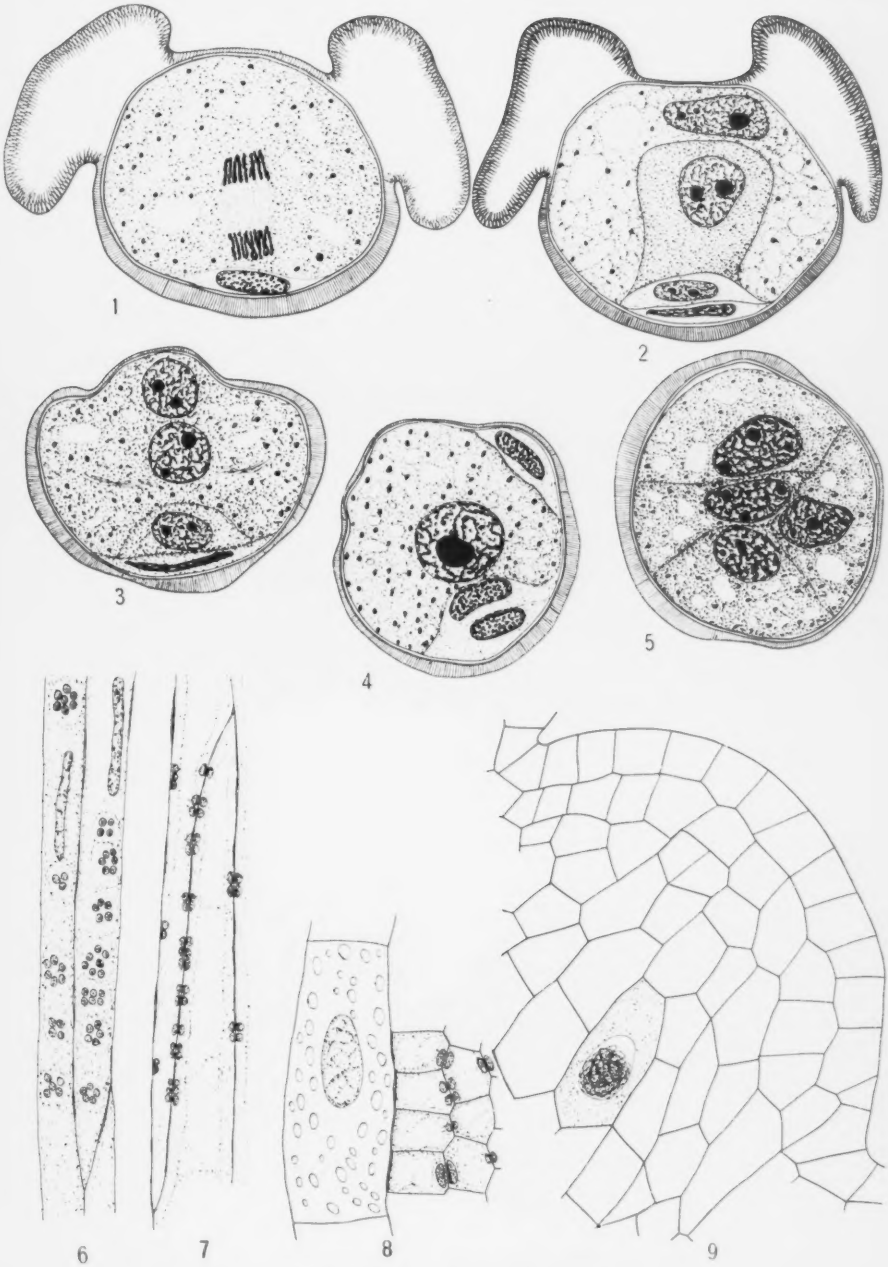
FIG. 21.—Junction of hollow meristematic cylinder of primary root and 4 meristematic regions of cotyledonary tube.

FIGS. 22, 23.—Cortex, region of meristem, and central axis.

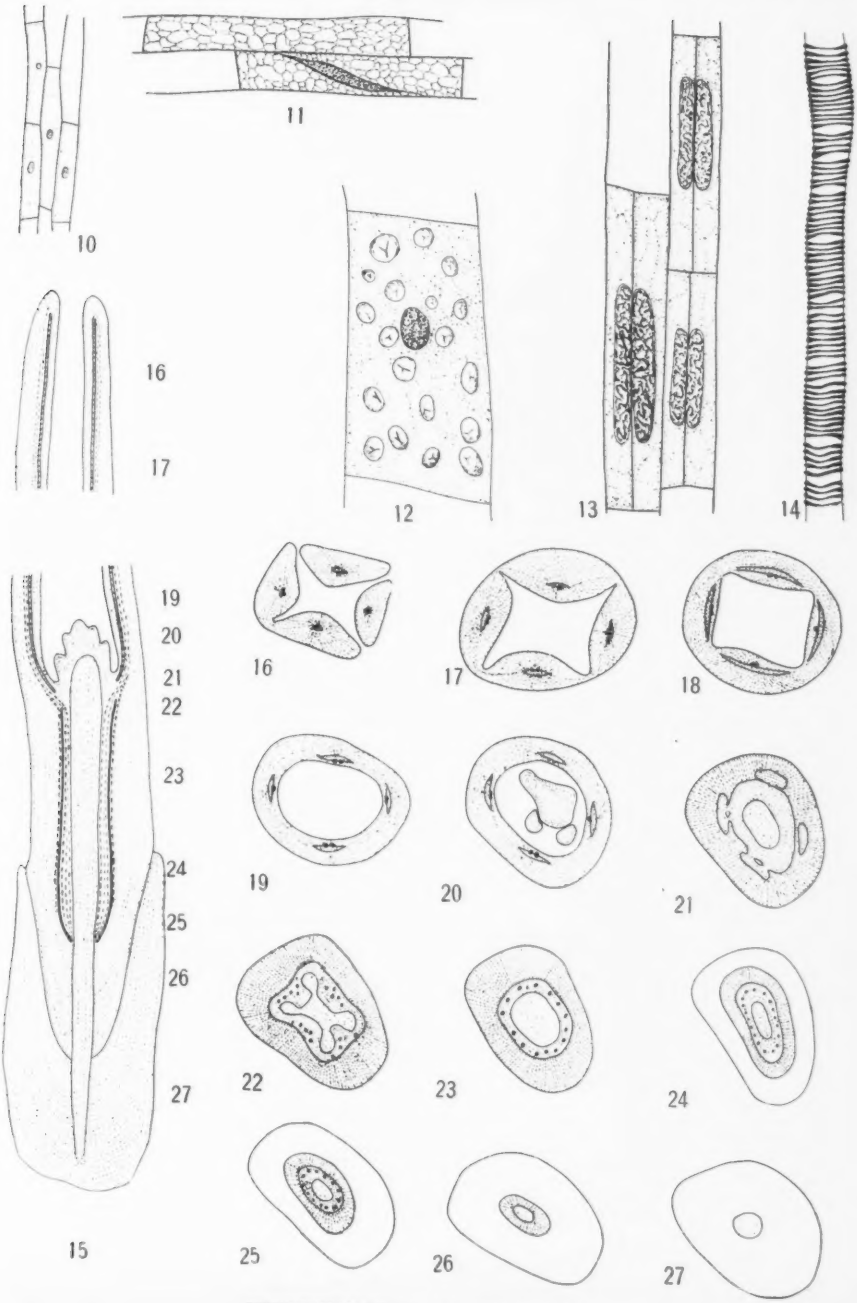
FIGS. 24, 25.—Showing 4 regions; coleorhiza, cortex, region of meristem, and mucilage tubes; also central axis.

FIG. 26.—Section of coleorhiza, cortex, and central axis.

FIG. 27.—Section of coleorhiza and central axis.



HUTCHINSON on KETELEERIA



HUTCHINSON on KETELEERIA

THE POLLINATION OF VALLISNERIA SPIRALIS

ROBERT B. WYLIE

(WITH PLATE IX AND SIX FIGURES)

Vallisneria has long been counted one of the classic examples of cross-pollination. Living vegetatively as a submersed aquatic, its dioecious flowers are brought together at the surface of the water in most ingenious fashion. These highly specialized flowers present the strongest contrasts, not only in size and structure, but in behavior as well, and give this plant its rank as one of the climax types with respect to floral differentiation. Specializations of such evident advantage for cross-pollination in a form so admirably situated for vegetative propagation seem to emphasize the importance of sexuality, or at least of seed production, in the higher plants.

While the general method of pollination in *Vallisneria* is well known, many interesting facts seem never to have been published, and the underlying principle has not been emphasized. The figures current in textbooks are highly generalized, and some of them are far from accurate. The story which they are intended to illustrate is likewise incomplete or in some cases highly distorted. In any event, neither figure nor story has done justice to the intimate history of pollen transfer in this remarkable plant.

It will be noted at once that the following account diverges radically from that suggested by KERNER'S (1) beautiful and widely copied figure. A comparison shows that these differences relate not only to the size and structure of the flowers, but are even more fundamental in character. KERNER emphasizes the fact that pollination is brought about through the contact of flowers floating on a level water surface; there follows an outline of a method of pollen transfer through the special agency of the surface film of water. The general drawing (pl. IX) is based on photographs of living flowers, measurements, and camera drawings of parts.

The epigynous seed-bearing flowers of *Vallisneria* are borne singly, each within its spathe at the end of a long scape, sometimes over a meter in length, which anchors the floating flower to the short upright stem at the bottom of the pond. Upon reaching the surface of the water through the elongation of this axis, the spathe opens at its outer end, but remains as a partial investment of the ovary until the seeds are nearly mature. The 3 spoonlike sepals soon separate, disclosing the 3 bifid stigmas which are coiled in the center of the flower (pl. IX). These fleshy stigmas are densely clothed with the stigmatic hairs, and their snowy whiteness constitutes the most conspicuous part of the flower. Rudimentary petals and slender staminodia are present, but as they seem functionless their discussion may be deferred to a subsequent paper.

The anchoring scape usually elongates sufficiently to permit the opening flower to assume an inclined position in the water as it is carried to one side by wind or current. The ovary, which is 20–25 mm. long before fertilization, is usually straight until the flower opens and has taken its position at the surface; later it often curves considerably in response to gravity, thus bringing the floral parts more nearly parallel with the surface of the water. This bending of the ovary at this stage is quite marked in plants growing in aquaria where the flowers are left undisturbed for some time.

The exposed floral parts are waxy and consequently are not wetted by the water, with the result that the flower comes to rest with a portion of its weight resting on the sepals and margins of stigmas supported by the surface film. This produces a slight depression of the water about the flower, perhaps 15 mm. in diameter, which is abruptly declined at its inner margin next to the pistillate flower. This sloping surface film plays an important part in capturing the floating staminate flowers, and later is intimately bound up with the actual transfer of pollen to the stigmas. Too much emphasis cannot be laid on the complete dependence of this plant upon the surface film of water for its pollination processes.

The staminate flowers are borne crowded numerously within the globose spathe which remains short-stalked at the bottom of

the pond. A count of several of these flower masses showed an average of over 2000 flowers packed within each spathe, the whole group the homologue of the single pistillate flower which is solitary within its spathe. The staminate inflorescence resembles a large fern sorus surrounded by an indusium. This similarity is carried further by the striking resemblance of the slender-stalked unopen staminate flowers to polypod fern sporangia. Massed within the spathe these flowers are joined to the axis by slender pedicels of varying length, so as to completely fill the space between the stem and the spathe.

The pollen-bearing flowers are very tiny, less than 1 mm. in diameter before opening, and are simple in structure. The floral parts consist of 3 sepals, 2 functional stamens, and rudiments of petals. The sepals are of unequal size and are not symmetrically disposed; 2 are similar and stand nearly opposite; while the third and smaller one is placed laterally between them. This reduced sepal is the first to open. Numerous tapering and curved hairs cover the region about the base of the stamens and are doubtless of some importance, although their functions are not clear. The 2 stamens stand close together and have their parallel filaments united up to a point near the anthers (pl. IX).

At maturity the tip of the spathe opens slightly and the staminate flowers begin detaching from their slender stalks. The uppermost are the first to be shed, and 2 or 3 days may be necessary to empty a single spathe. These detached flowers rise slowly through the water to the surface and there very slowly open. In this respect *Vallisneria* stands in sharp contrast to the writer's (2) observations on *Elodea canadensis*. In that form the staminate flowers upon release dart to the surface and there fairly explode, scattering their pollen on the surface of the water. In *Elodea*, however, it is the free floating pollen that functions, while in *Vallisneria* the pollen retained in the anthers has the better chance of reaching the stigmas. SVEDELIUS (3) reports that the sepals of the detached staminate flowers of *Enalus acoroides* snap back upon reaching the surface of the water, although the pollen is retained in the anthers. In *Elodea canadensis*, and perhaps in *Enalus*, the snap of the sepals seems to be due in part at least to the release of

gases imprisoned between the floral parts under water. The writer (4) has noted elsewhere that in *Elodea ioensis*, which has a long-stalked staminate flower, a bubble of gas is generally associated with the partly opened sepals, giving extra buoyancy to the submerged flowers, which tug at their anchorage like captive balloons.

No prolonged observations were made on the possible periodicity in the release of the staminate flowers of *Vallisneria*, although doubtless there is a relation between their detachment and the gases given off by the plant during times of brighter illumination. On one occasion it was observed that as the sun came up from behind a building and its direct rays fell on the spathe of the staminate inflorescence the rate of detachment was considerably increased for a time. In *Elodea canadensis* (2) there is a correlation between the coming of strong light in the morning and the rate of detachment of the staminate flowers. SVEDELIUS reports that the staminate flowers of *Enalus acoroides* are released mainly (if not exclusively) at periods of low tide. This habit is of peculiar significance from the fact that at high tide the pistillate flowers of that plant are wholly submerged and pollination would be impossible. No explanation of this relation was suggested in the paper.

The sepals of the staminate flower of *Vallisneria* completely invest the stamens until some time after the flower reaches the surface. They then slowly recurve, the smaller one being first to open (pl. IX), and as it touches the water it seems to function in orienting the flower so that when the pair of lateral sepals open there are formed 3 boatlike structures which engage the surface film and float the flower. This tiny flower, with its upraised stamens and pollen mass, is so snugly fitted to the surface film by its 3 broad areas of contact that it is kept in equilibrium under all ordinary circumstances. They are rarely overturned, even by rather vigorous agitation of the water, but maintain a strict right angle to the surface film. So slender an object as a needle if thrust into the water among these floating flowers and slowly withdrawn will be covered by the flowers that have been drawn up with the film of water about the needle and may be seen standing out radially from it on all sides. Once overthrown, however, they are not again righted, but lie partly under water.

This definite engagement with the surface film does not hinder the free movement of the staminate flowers on the water. In open areas they are caught by every passing breeze and are hurried along the surface of the water. On windy days they go scudding by the observer like tiny flecks of foam. Where the plants grow abundantly they often mass along the windward shores in broad zones of snowy white (fig. 1).

The anthers dehisce before the flowers open, and the sticky pollen from the pair of stamens of a given flower usually forms a single pollinium (pl. IX). Even if the products of the 2 anthers form

FIG. 1.—Floating staminate flowers along margin of East Okoboji Lake in northwestern Iowa; the dead fish shown near center of picture was about 8 inches long.

separate pollen masses, these lie so close together as to be practically tangential, and are never widely separated, as shown by KERNER (1). Seen under moderate magnification these masses of pollen gleam like clusters of pearls. The microspores, which are slightly oval in form, are about 65 μ in diameter and have a nearly smooth exine. Their adhesiveness is of great advantage in holding the pollen together until it is rubbed off against the stigmas, and doubtless assists after pollination in holding the spores to the stigmatic hairs. The pollen output is limited, averaging about 100 spores to the flower, but varying considerably.

The floating staminate flowers are carried along by the wind, and coming within the radius of the declined surface film about the pistillate flower slide into the little depression, where they are

retained. In this manner possibly as many as 50 staminate flowers may be caught in a single depression, thus forming conspicuous white patches on the surface of the water. It is interesting to note how successfully these areas of associated flowers hold together even when the water is quite rough. COWLES (5) mentions these film pockets, but gives no details other than to compare them with those of *Elodea canadensis*. In this latter form, as previously described (2), the floating pollen grains are caught in the depressions that are formed about the tiny pistillate flowers. SVEDELIUS speaks of a similar "capturing" of the pollen-bearing flowers in *Enalus acoroides*, but does not attribute this to the influence of the surface film, although obviously the case closely parallels that of *Vallisneria*.

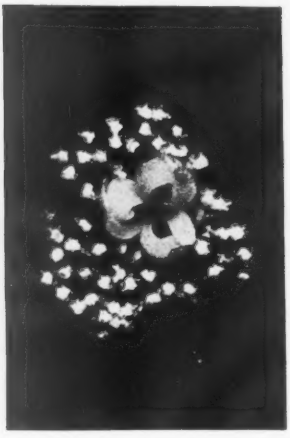


FIG. 2.*—Flowers floating on surface of water in a small aquarium surrounded by black paper; pistillate flower in center.

The sepals of the innermost of the captured staminate flowers in *Vallisneria* are of course in contact with the margins of the pistillate flower (fig. 2), but later arrivals are held back as they form only a single layer in the depression. It should be noted at this time that contact between flowers on a level water surface, such as KERNER figures, could not lead to pollen transfer, as the pollinia are upraised over the center of the flower. But with any slight declination of the film about the pistillate flower, even in quiet water, there might be contact between the innermost pollinia and the stigmas (fig. 2). Obviously, however, any movement resulting in a further depression of the pistillate flower would cause the surface film to become more abruptly declined, thus tipping the staminate flowers more sharply inward (fig. 3) and thereby

* FIGS. 2–6 constitute a series illustrating changes in relations of associated flowers floating at surface of water when subjected to submergence by pulling on scape of pistillate flower.

making conditions more favorable for pollen transfer. The upward movement of the water due to a passing wave might serve to temporarily depress the floating pistillate flower weighted by its long stalk. Should the movement be sufficient to make taut the anchoring scape, even for an instant, the depression would become cuplike, with the inner staminate flowers standing at right angles to its nearly vertical walls (fig. 4). Many of the pollen masses would thus be forced directly into the stigmas, although the outer ones would still be held back at some distance. At a certain stage of depression, however, the lateral pressure of the water breaks the surface film above the flower; the sides of the cup snap together, roofing it over; and a considerable number of staminate flowers, with the pistillate flower, are thus shut tightly together in a common bubble beneath the surface of the water (fig. 5). It should be noted that this process has completely overturned the staminate flowers, and that these are now inverted upon the pistillate flower, with their pollen masses pressed sharply into the stigmatic surfaces. The photograph for fig. 5 was taken through perhaps a centimeter of water, and shows the out-turned bases of the staminate flowers lining the bubble as seen from above. To the right may be seen a number of free floating staminate flowers that were released from the depression as the flowers disappeared beneath the surface.

FIG. 3.—Positions assumed with slight tension on scape of pistillate flower.

Release of the tension on the scape permits the flowers to come again to the surface; the bubble breaks, and most of the flowers resume their original relations at the surface of the water (fig. 6). Examination, however, shows numerous pollen grains or even entire staminate flowers scattered over the surface of the stigmas. Fig. 6 shows that the group of free floating staminate flowers,

released when the group was submerged, has again entered the film pocket. This resulted from being blown into the radius of the declined surface.

Each passing wave thus brings a shift in the position of the flowers and furthers the wearing away of the pollinia upon the stigmas. During the time that the pistillate flower is at the surface the events outlined may be repeated hundreds of times with varying degrees of submergence. At all times, of course, there may be additions to the group from the free floating staminate flowers. Attention should be directed to the fact that any degree of depression is helpful, and that complete submergence, although this probably occurs frequently, is not necessary to adequate pollination.

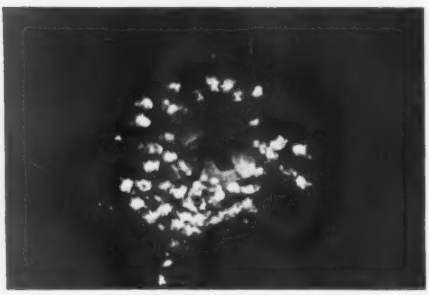


FIG. 4.—Pistillate flower has been pulled farther down in water; depression is cup-shaped, and staminate flowers stand at right angles to the verticle walls.

When the pistillate flower is finally withdrawn into the water by the coiling of the scape, numerous pollen-bearing flowers may be trapped in the bubble of air that forms about the retreating floral parts as they disappear beneath the surface. As the volume of imprisoned air is gradually dissolved by the water, the pollinia would be pressed more and more strongly into the stigmas. Observations on isolated patches of pistillate plants show that the scapes will coil somewhat without pollination, so the retreat of the seed-bearing flower is the final step in pollination if the pollen-bearing flowers are present. At the first favorable opportunity the writer plans to make a study of the flowering habits of marked plants in the field to determine the length of time the flowers remain at the surface, and the influence of pollination upon the time of their retreat.

Despite the dioecism and complete separation of the flowers in *Vallisneria*, pollination seems to take place with remarkable

certainty, provided both kinds of flowers are near together in the same body of water. No doubt the pollen-bearing flowers often ride the surface of the water for considerable distances. They will float for days, and the pollen seems to withstand desiccation for a long time. In our laboratory aquaria the decline of microspores seems to be due to the attacks of fungi, and collections from the field often show hyphae among the spores.

From 200 to 450 ovules line the walls of the ovary, so that the entire pollen output of several staminate flowers would be necessary for fertilization, even if all the spores germinated. Fertilization seems to take place with certainty, for few ovules fail to develop into seeds. Scores of supernumerary pollen tubes are frequently seen lining the walls or wandering through the ovarian chamber among the ovules. Many of these meandering pollen tubes form enlargements at their distal ends similar to those previously reported for *Elodea canadensis* (**2**).

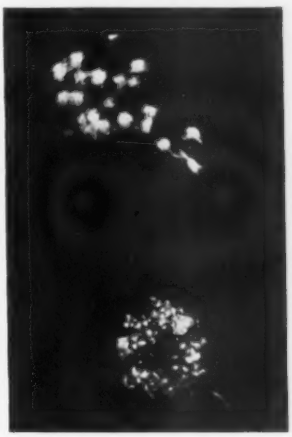


FIG. 5.—With further depression the water has closed over the flowers, now shut together in a common bubble; out-turned bases of staminate flowers may be seen on all sides, while pollen masses are being pressed directly into stigmas; near by are some pollen-bearing flowers that escaped when others were caught in the bubble (these moved during time of exposure and so are blurred in picture).

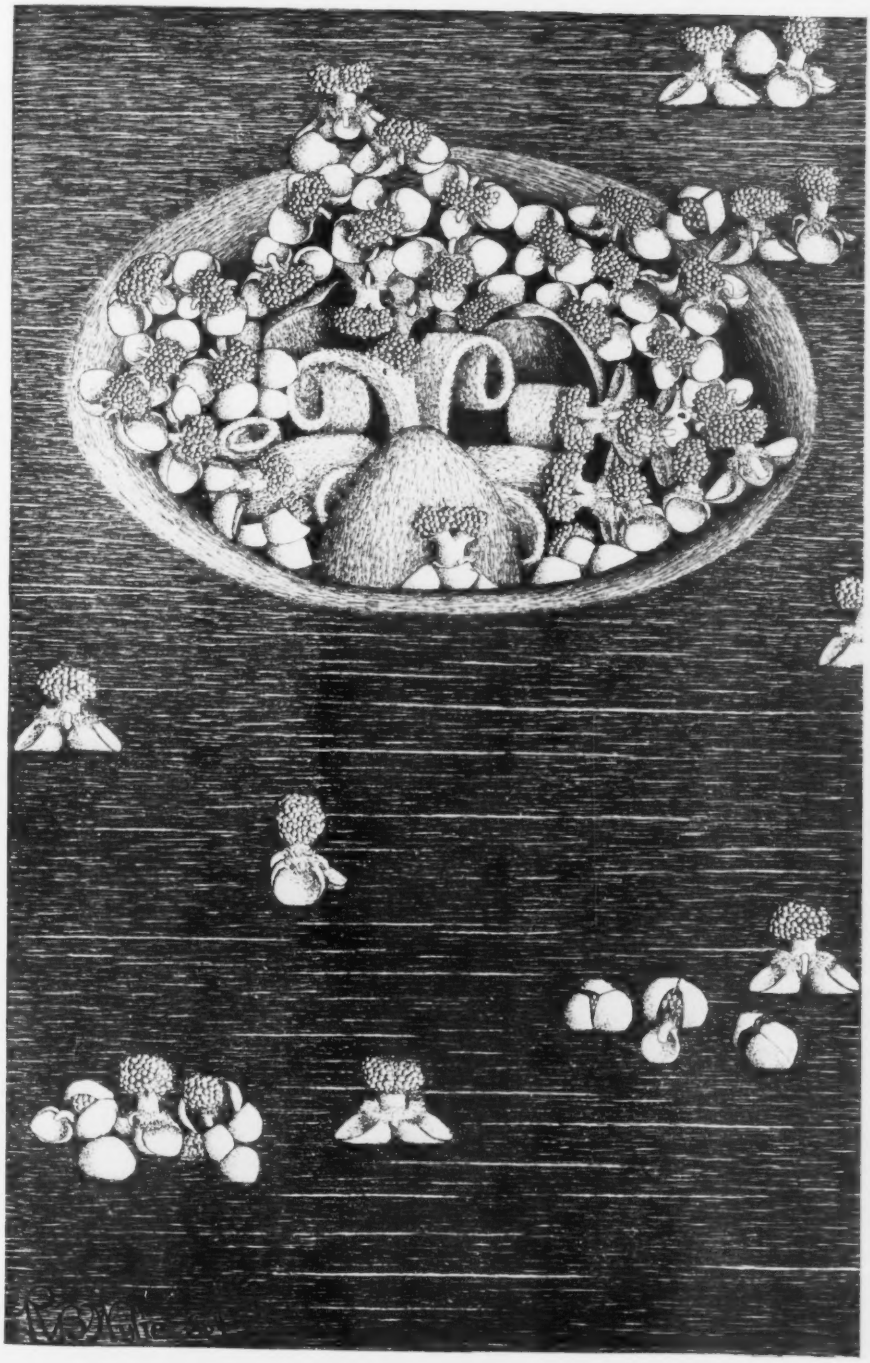
Turning now to KERNER'S widely copied figure illustrating his description of the pollination of *Vallisneria spiralis*, one is struck by the many points of contrast with the foregoing account. His illustration shows a pistillate flower with long slender ovary which, relative to the spread of the floral parts, is only about one-third of the diameter of that in our form. The spathe invests only the base of the ovary, whereas in ours it extends up almost to the sepals. The wide-spreading sepals are shown as straight, while the broad stigmas are flattened, outstanding, and raised entirely above the surface of the water. The stigmas, as shown in the

figure, have margins fringed with long hairs and spread much more widely than in our plant. Finally, the whole pistillate flower in KERNER's figure is placed in such relation to the surface of the water that it could be sustained there only on the supposition that it is supported by a stiff stem.

Similarly, KERNER has figured the staminate flower as markedly different from ours. It is represented as having 3 equal and symmetrically arranged sepals; the stamens are figured with long filaments at right angles and protruding beyond the margins of the sepals. Tiny clusters of pollen grains crown these wide-spreading filaments, carried after the fashion of the spar torpedo well over the margins of the flower. Compared with its companion blossom, the staminate flower is figured as many times larger than in our plant.

FIG. 6.—Release of tension on the scape has permitted submerged flowers to come again to surface; pollen and some entire staminate flowers may be seen on stigmas.

These and many other minor points of difference suggest that KERNER's account is highly generalized, and perhaps intended to convey only a general account of the pollination in this plant. It may only be accidental that most of the departures from the conditions found in our plant are necessary to make possible his proposed plan of pollen transfer. On the other hand, it may be that the European plant is essentially different from ours of the same name; if so, ours should be described as another species. That there may be considerable difference between the forms on the two continents is further supported by TURPIN's (**6**) figures, which show slender stamens somewhat divergent, and stigmas very different from those found in our form. In so far as one can depend upon published figures, it would seem that rather widely divergent plants are included in the species *Vallisneria spiralis*.



WYLIE on VALLISNERIA

The writer would welcome photographs, drawings, or specimens from distant regions for purposes of comparison.

In conclusion, it seems clear that *Vallisneria* offers a remarkable series of specializations mainly related to pollination at the surface of the water. A few aquatic plants have solved the problems of pollen transfer under water, and so may carry out their entire life history as submersed plants. A good example is seen in *Ceratophyllum demersum* L., which is pollinated below the surface and so may flourish at considerable depths in clear water. Neither *Vallisneria* nor *Elodea* shows any evidence of transition to subsurface modes of pollination, although this would seem to be a desirable goal for all aquatic flowering plants. On the contrary, they are perhaps carried further and further from this possible habit by their devices favoring pollination in air. Their specializations not only bespeak long association with water, but also constitute a remarkable series of adaptations to pollination at its upper limit through the agency of the surface film.

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EXPLANATION OF PLATE IX

A general drawing representing a group of associated flowers as they appear when slightly depressed; free floating staminate flowers outside the depression.

TOLERANCE OF FRESH WATER BY MARINE PLANTS AND ITS RELATION TO ADAPTATION

W. J. V. Osterhout

Some effects of distilled water on protoplasm have been described by the writer.[1] Further investigations on this subject have shown remarkable differences between marine plants, and even between different cells of the same plant, with respect to their tolerance of fresh water. These differences are interesting from a physico-chemical standpoint, and significant because of their bearing on the theory of adaptation.

It is commonly supposed that most marine plants are killed by exposure to fresh water.[2] Some instances have recently come under the writer's observation in which death occurs with great rapidity. A good example of this is furnished by *Polysiphonia violacea*. Upon placing it in pure distilled water, many of the cells are killed within a minute. This is clearly shown by the fact that if they are replaced in sea water at the end of a minute they become disorganized and never recover. This effect of distilled water is not due to the presence of toxic substances acquired during distillation, for the water was prepared with especial precautions and was not toxic to sensitive species of *Spirogyra* and to sensitive root hairs. Moreover, the same effect is produced by water taken directly from ponds, rivers, and springs.

On the other hand, there are species which are quite tolerant of fresh water. Some years ago the writer[3] found marine algae growing along the sides of a steamboat. These were exposed alternately for some hours each day to salt water and to fresh water. They were also exposed daily to concentrated sea water and to strong sunlight, under which they reached a relatively high temperature. They included representatives of the red, brown, green, and blue-green algae, and were associated with a somewhat varied

[1] Bot. Gaz. **55**:446. 1913.

[2] Cf. Pfeffer, Pflanzenphysiologie **1**:415.

[3] Univ. Calif. Publ. Botany **2**:227. 1906.

fauna. One who is inclined to attribute this remarkable tolerance of fluctuations in salinity to a process of gradual adaptation will meet with many difficulties.

The writer recently had an opportunity, on the island of Mount Desert, Maine, to observe plants which are subjected to both fresh and salt water. At the mouths of brooks, in situations between tide marks which are exposed alternately to 6 hours of fresh water and to 6 hours of salt water,[4] there flourishes a surprisingly large flora, including representatives of the red, brown, green, and blue-green algae, and a flowering plant, the eel grass (*Zostera marina*).[5]

In some places tide pools are found in the beds of brooks. When the tide is out these pools are filled with salt water except for a layer of fresh water which rests on the top of the salt water and flows in a gentle current over it. The depth of the fresh water may be as much as 7 inches, and that of the salt water 2 or 3 feet. The line between the two layers is sharply marked.[6] In such places one portion of a plant may be exposed for several hours a day to fresh water, while the remaining portion is always in salt water. There seemed to be no differences between these portions of the plant.

What enables these plants to survive under such unusual circumstances? The current explanation is that they have gradually adapted themselves to these conditions. The eel grass might be

[4] As soon as the plants are covered with salt water by the rising tide, the fresh water no longer affects them, since it flows over the surface of the salt water without mingling much with it.

[5] Among the species which endure 6 hours of fresh water alternating with 6 hours of salt water may be mentioned the following, which were kindly identified by Dr. W. G. FARLOW: *Gomontia* sp., *Enteromorpha intestinalis*, *Monostroma Blyti*, *Fucus vesiculosus*. Some of these species, for example *E. intestinalis* and *M. Blyti*, endure much greater exposure to fresh water. Mr. F. S. COLLINS has noted that *Ilea fulvescens* (Rhodora **5**:175 and **6**:20; also Green algae of N.A., p. 206), *Enteromorpha micrococca* (Torr. Bull. **18**:336; also Green algae of N.A., p. 204), and *Pilinia minor* (Green algae of N.A., p. 292) stand exposure to fresh water. See also PFEFFER, Pflanzen-physiologie **1**:415 and OLTMANNS, Morph. u. Biol. der Algen **2**:173–183. 1905.

[6] Small animals in these pools (*Gammarus*, young eels, etc.) swim back and forth from one layer to the other without any sign of inconvenience. The boundary between the two layers is easily made visible by stirring; water-logged vegetable matter taken from the bottom of a fresh-water pool sinks to the boundary and remains there.

cited as an especially good example; its leaves are exposed alternately to fresh and salt water, but its roots, being covered by mud, are exposed to comparatively little change in salinity. The theory of adaptation might lead us to expect that the leaves of such plants would be much more tolerant of fresh water than the roots. This expectation is most strikingly confirmed by experiments, which show that the root cells of these plants are killed by fresh water in a few minutes, while the leaf cells can stand exposure to fresh water for several hours. But the argument must be reversed as soon as we make experiments with specimens of eel grass taken from salt water in places remote from the mouths of streams, where no opportunity for adaptation to fresh water occurs. In these plants we find the same differences between root and leaf with respect to their ability to withstand fresh water that we find in plants growing at the mouths of streams.

We must suppose, therefore, that characters which seem to be the result of adaptation were in this case present from the beginning and must be ascribed to entirely different causes. Doubtless this is also true of many cases which at present serve as typical instances of adaptation.[7]

There is much significance in the fact that leaf cells may withstand a much longer exposure to fresh water than the root cells of the same plant. One might be inclined to explain this by differences in the cell wall rather than by differences in the protoplasm, particularly as the cell wall in the root is usually more permeable to water than the cell wall in the leaf. It is clear that this is not the case here, however, for when leaf cells and root cells are placed side by side in hypertonic sea water, they are plasmolyzed with equal rapidity, and when replaced in ordinary sea water they recover at the same rate; this shows that their permeability to water and to the salts in the sea water is about the same in both cases.

Another consideration shows that the difference in the behavior of the cells cannot be due to differences in their permeability to water. This is the fact that death is not primarily due to absorp-

[7] Experiments with other species growing at the mouths of brooks showed that individuals which have had no opportunity for adaptation to fresh water show a great tolerance of it.

tion of water. In the process of dying the majority of cells exhibit little or no increase in size, showing that they absorb little or no water. Certain exceptional cells may swell and even burst, but this is not the rule.[8] Moreover, the cells die in isotonic cane-sugar solutions, although not as rapidly as in distilled water.[9]

We must look, therefore, for another explanation of these effects. It has been pointed out by LOEB that when death occurs in distilled water it must be due to diffusion from the protoplasm of substances which are necessary to its normal activity, and that doubtless the most important of these are inorganic salts. The reason why some protoplasm is more tolerant of distilled water may be that it parts less readily with certain salts which are combined (chemically or mechanically) with it.

It may also be true that the less tolerant protoplasm consists more largely of substances (globulins or other colloids) which undergo a change of state as soon as the concentration of salts falls below a certain limit. In order that the cell should be intolerant of distilled water the globulin (or other substance) need not constitute a large part of the protoplasm, for it might, even in small quantity, play an extremely important rôle, such as that of a protective colloid or of a constituent of the plasma members. These effects would be very simply explained by such an assumption.

LABORATORY OF PLANT PHYSIOLOGY
HARVARD UNIVERSITY

[8] In some cases failure to swell may be due to the rigidity of the cell wall, but certain cells which have no rigid cell wall fail to swell under these conditions.

[9] This has been shown for certain animal cells by LOEB, Pflüger's Archiv **97**:406, 1903.

BRIEFER ARTICLES

HENRY HAROLD WELCH PEARSON

(WITH PORTRAIT)

Professor H. H. W. PEARSON, professor of botany in the South African College at Cape Town, died November 3, 1916. He was born at Long Sutton, England, in 1870, and was educated at Cambridge, receiving the M.A. degree in 1900 and the Sc.D. in 1907. He was assistant curator of the Cambridge herbarium from 1898 to 1899, and then went to the Kew Gardens where he remained until 1903. From Kew he went to the South African College, where his principal work was done. His thorough training in taxonomy enabled him to utilize at once the opportunity of a rich and little studied flora, and he made numerous contributions to the *Flora of South Africa*, *Flora Capensis*, *Philosophical Transactions*, *Geographic Journal*, *Annals of Botany*, and other periodicals. His researches were not confined to taxonomy. There were ecological papers upon South African cycads and morphological studies of *Welwitschia* and *Gnetum*, two genera in which he was so deeply interested that he not only spent a great deal of time and money, but eagerly endured the hardship of collecting material in distant and almost inaccessible places.

In a letter dated September 8, 1916, he states that he has in press two papers on *Gnetum*, and that he was to make another trip to Damara-

land in January to study *Welwitschia* and get material for further investigation. In the same letter he writes: "I don't think there is the least chance for peace before September, 1917. I wish I could get away from present occupations and take a part, but I am not encouraged by the authorities."

Five years ago, while studying cycads in South Africa, it was my good fortune to become acquainted with Professor PEARSON, and to be entertained in his home. He was a vigorous, kindly man, intensely interested in his work and enthusiastic over the botanical possibilities of South Africa. During a stroll on Table Mountain he pointed out to me a magnificent site for a botanical garden, at that time only a dream or a vision; but with him a vision was followed by meditation, and then by determined effort to make his dream come true. The visions which he saw during such strolls have materialized in the National Botanic Gardens at Cape Town, with an unsurpassed location, and with such a rapidly growing collection of plants that the place is already one of the great gardens of the world.

By his untimely death—he was only 46 years old—science has lost a great botanist, but it is to be hoped that his high ideals of scientific work will still remain to guide the botanical policies of South Africa.—CHARLES J. CHAMBERLAIN, *University of Chicago.*

SOIL MOISTURE INDEX

Outdoor botanists in thinking of any plant are likely to associate with it some measure of its soil moisture relation. The terms xerophyte, mesophyte, and hydrophyte naturally come to mind, or at least the conceptions that these names connote. With college students, however, no such association of ideas is likely to occur unless special attention is directed to the subject. This may be done by requiring the student to examine the habitat, note the associated species, and estimate the water requirements. Such a plan was tried the past summer at the University of Colorado Mountain Laboratory at Tolland, Colorado. For this purpose a scale, which may be called a "soil moisture index," proved useful. A rule of the laboratory required that every plant studied should be recorded with an index number, this to be criticized and perhaps altered by the instructor.

The index numbers form a scale from 1 to 10 with the following significance: (1) lithophytes; (2) plants of driest, sterile soil; (3) hyperxerophytes; (4) xerophytes; (5) xero-mesophytes; (6) mesophytes;

(7) plants of wet meadows or moist forest; (8) marsh plants; (9) plants partly submersed; (10) plants growing in water.

In using the index most plants will be grouped around 4, 6, 8, and 10. This will be the case especially with students who have had little experience in field work. Later, when a finer discrimination is developed, the intermediate numbers will be employed more often. If extreme nicety is desired, decimals may be used. They will be satisfactory in the study of some particular community, as a meadow or a prairie, in which the student becomes acquainted with relative moisture requirements of a number of species. If less accuracy is required, plus and minus signs furnish a useful means of distinction. Thus, the elms may be called no. 6, the red maple 6+, and the red oak 6−. Students in desert and arid regions will need to work out the meanings of the index figures 2 and 3. Others will probably be content with calling all xerophytes no. 4. A plant that occurs in a number of different habitats may be indicated by two or more numbers, as, for example, *Achillaea lanulosa* 6, 7, 8.

There is no deep philosophical conception underlying the use of the scale and no instrumentation is intended in connection with it. It merely emphasizes the importance of water in the substratum and furnishes a suitable terminology for description and a vocabulary for thinking about soil moisture relations. It is possible that in research work on floristics the use of this or some other suitable scale may be found desirable. Perhaps workers in different localities might agree on typical plants to represent the different index numbers. The scale may well be used for a better understanding of transition areas, such as occur between meadow and marsh or between meadow and dry grassland. Any piece of vegetation may be given an index number if the indexes of its component species (previously determined in other situations) be averaged. Thus one might recognize a no. 6 meadow, a no. 6.5 meadow, or a no. 7 meadow.—FRANCIS RAMALEY, *University of Colorado, Boulder, Colorado.*

CURRENT LITERATURE

BOOK REVIEWS

Evolution

A book by LOTSY[1] is the most recent contribution to the literature of evolution. The author is evidently handicapped by the intricacies of English spelling and punctuation, for there are scores of instances of misspelled words, incorrect punctuation, and faulty idiom. It is to be regretted that these types of elementary error were not eliminated by the publisher, for the book-making is otherwise excellent. Perhaps the commonest error is that of ignoring the accepted canons of word division at the end of a line. With great frequency monosyllabic words are divided and words are broken in the middle of a syllable. Unfamiliarity with English idiom also leads frequently to strikingly awkward expressions. For example, on page 29, the following meaningless sentence occurs: "This species undoubtedly are in an uninheritable way." On page 120 this paragraph occurs just as quoted: "While hare and rabbit don't pair in nature, a male hare doubtless would do so if sufficiently long isolated with female rabbits, in the absence of male rabbits on an island, as ressorts from the experiments of Mr. Houwink, showing that the hare looses its inborn aversion of a tame rabbit, if it is taken soon after birth from its mother, and sucked by a tame rabbit foster-mother." Similar passages are frequent.

Another peculiar type of error is in the use of "e.g." and "i.e."; for the author reverses our usage constantly. He has also invented another abbreviation which serves him well, using "f.i.," apparently for "for instance." Not infrequently Dutch and German words are substituted for English, as "bij" for "by," "unter" for "under," and "alle" for "all." Any English writer, in an evening's work, could have edited the book into acceptable form and it is to be regretted that some such editing was not done.

Apart from these most obvious mechanical imperfections the book is of considerable interest, in that it serves to emphasize the importance of hybridization as a factor in evolution. The author's position, however, is an extreme one, in that he holds hybridization to be the sole cause of variation. The principal ideas that form the backbone of his argument are as follows.

1. Linnean species, or *Linneons* as he calls them, are not species at all, but artificial groups of intercrossing types, that are constantly giving Mendelian ratios. All so-called mutations are merely extracted recessives, which if isolated produce new pure types.

[1] LOTSY, J. P., Evolution by means of hybridization. 8vo. pp. viii+166. The Hague: Martinus Nyhoff. 1916.

2. A real species is "a group of individuals of identical constitution, unable to form more than one kind of gametes; all monogametic individuals of identical constitution consequently belong to one species."

3. A "Linneon," says Lotsy, "is a vestigial group of a once much larger group of differently constituted types, born of a cross, which is apt to simulate a species by the overwhelming majority of the dominant types it contains, as a result of free-intercrossing, combined with a favoring of the dominants by a process of selection, weeding out the weaker or more conspicuous recessives; this uniformity being more apparent then real, because pure dominants are indistinctible, in most cases, from dominant-hybrids."

4. In another place the author states briefly his idea of the causal factors of evolution. "The vera causa of the production of new types consequently is: crossing; the vera causa of their extinction: the struggle for life; the selection resulting from the latter is by no means a revival, but is the sign of the struggle of the doomed." Just what is meant one can only conjecture by the context.

In taking the position that no variations or mutations arise except as the result of crossing and subsequent segregation, the author throws out of court the mutants that have arisen in such carefully controlled experiments as those of MORGAN and his pupils on *Drosophila*. He challenges the reader to produce a single case of mutation in a true species, which, according to him, is a type that produces only one kind of gamete and shows no variability in F_1 and F_2 generations. In other words, if a mutation does occur it may be taken as prima facie evidence of impurity in the stock. Such an argument leads nowhere.

The author follows his theory to its logical conclusion and attempts to show that even classes and orders must have been the result of crossing. We fail to see the necessity of forcing a theory, that seems fairly reasonable when applied within limits, to such an absurd length. If we object, we are told that "a formation of new classes is not in action at the present moment, so that it is illegitimate to claim that one who wants to explain evolution must demonstrate how such a formation of new classes goes on."

In conclusion, the reviewer would like to recommend the reader to the second edition of this book, which, if it ever appears, will doubtless be a considerable improvement on the first.—H. H. NEWMAN.

MINOR NOTICES

Forestry for boys.—In a volume dedicated to the youth of America and to the leader of the Boy Scouts, MOON[2] has described in a readable manner the problems and processes of tree growth, forest development, and forest utilization. The extent and economic value of our forests are well emphasized

[2] MOON, F. F., The book of forestry. 8vo. pp. xvii+315. *figs.* 64. New York: Appleton. 1916. $1.75.

and the importance of their conservation made clear. The harvesting and utilization of the timber crop is described in an interesting manner, as well as the training and duties of the forester. Some attention is given to such forest industries as maple sugar making, nut growing, resin production, and wood distillation. A word is said about the value and care of shade trees, and a glance is taken at the future possibilities of forestry, everything being treated in a non-technical way likely to interest the "Boy Scout" and many of his elders. The latter part of the book is devoted to very brief descriptions of some 50 trees, each being illustrated by a small drawing of leaves and flowers or fruit.

While neither a textbook nor a scientific treatise, it is interesting and seems well suited to the purpose of interesting the public and more particularly the boys, in the forest and the forester as they concern the happiness and prosperity of our land.—GEO. D. FULLER.

Soil bacteriology.—A laboratory manual of soil bacteriology by FRED[3] is intended as a guide to teachers and students in courses given in soil bacteriology. The subject is logically developed and directions are given in clear, concise form. There is perhaps no branch of bacteriology so intimately associated with chemistry as soil bacteriology, and therefore considerable attention is given to this phase of the subject. There are a number of excellent illustrations in the book, and one of the most valuable features is the fairly complete assortment of recipes for preparing culture media suitable for the study of soil bacteria. Special sections deal with methods of quantitative and qualitative chemical methods of analysis. Provision is made at the conclusion of exercises for the student to record results in tabular form, a feature which adds materially to the value of the book.

It is being realized in agricultural schools that the study of soil bacteriology is of eminent importance, and this manual will undoubtedly be appreciated by those interested in such courses.—P. G. HEINEMANN.

North American flora.—The first part of Vol. 21 begins the Chenopodiales by presenting the Chenopodiaceae monographed by STANDLEY.[4] There are 105 species recognized, distributed among 27 genera. A new genus (*Meiomeria*) is based upon *Chenopodium stellatum* S. Wats. The large genera are *Atriplex* (96 species, 20 of which are new), *Chenopodium* (52 species, 13 of which are new), and *Dondia* (20 species, 7 of which are new). New species are also described in *Salicornia* (2) and *Endolepis*. One of the remarkable features of the family is the number of small genera, 13 being represented by a single species, and 4 by 2 species. In fact, 177 of the 195 species are included in 4 of the 27 genera.

[3] FRED, EDWIN B., A laboratory manual of soil bacteriology. 12mo. pp. 170. Philadelphia: Saunders Co. 1916. $1.25.

[4] North American Flora **21**: part 1. pp. 1–93. Chenopodiales: Chenopodiaceae, by P. C. STANDLEY. New York Botanical Garden. 1916.

The sixth part of Vol. 9 concludes the presentation of the *Agaricaceae* by MURRILL,[5] 5 genera being presented, which include 165 species, 16 of which are described as new. The largest genus is *Clitocybe*, with 88 species and including 13 of the new species. The part closes with a list of corrections and a bibliography for the volume.—J. M. C.

Jackson's glossary.—A third edition of this well known volume has appeared.[6] The development of subjects in botany and the consequent growth in terminology has made a new edition imperative. Especially is this true in reference to the numerous "recently coined terms" in ecology. No glossary can be perfect, and it would be easy to pick flaws in this one, but it must be regarded as complete and trustworthy as such a book can be. It contains approximately 21,000 terms, so that it must be fairly representative of botanical terminology. With the increasing number of special fields of botany, even a trained botanist needs a convenient glossary on his shelves.—J. M. C.

Correspondence of Linnaeus.—Under the editorship of HULTH, the correspondence of LINNAEUS is to be published in a series of volumes, the first one of which has just appeared.[7] The collection includes letters "from and to" LINNAEUS. The extent of the correspondence is indicated by the fact that this first volume, of over 400 pages, includes 49 correspondents listed under the first two letters of the alphabet. Most of the letters are in Latin, and give an intimate and interesting picture of the biology and biologists of the Linnaean period.—J. M. C.

NOTES FOR STUDENTS

Cecidiology.—Three interesting American papers on the histology of galls have been published recently and demonstrate the increasing interest in the study of pathogenic structures.

STEWART[8] presents a very interesting paper on the anatomy of *Peridermium* galls. The studies were made from *Peridermium cerebrum* Pk. on *Pinus Banksiana* Lamb. Galls of various ages were used, but all of them from young branches. It appears that the infection usually takes place during the first year's growth of the shoot. The woody portion of the gall was very distinct from the normal tissue. The author summarizes his results as follows:

[5] *Op. cit.* Agaricaceae, by W. A. MURRILL. **9**:375–426. 1916.

[6] JACKSON, BENJAMIN DAYDON, A glossary of botanic terms, with their derivation and accent. 8vo. pp. xii+428. Philadelphia: Lippincott. 1916. $3.00.

[7] HULTH, J. M., Bref och Skrifvelser af och till CARL VON LINNÉ. Vol. I. ADANSON-BRUNNICH. 8vo. pp. viii+429. Upsala: Akademiska Boktryckeriet. 1916.

[8] STEWART, ALBAN, Notes on the anatomy of *Peridermium* galls. Amer. Jour. Bot. **3**:12–22. 1916.

"(1) both an alternate and an opposite arrangement of bordered pits in the radial walls of the tracheids; (2) an unequal thickening of the walls and lumina of the tracheids; (3) very short tracheids with blunt end walls, which resemble parenchyma cells except in the pitting; (4) cells which are transitional between tracheids and parenchyma cells in the pitting; (5) the presence of true wood parenchyma cells; (6) a small production of thin-walled summer tracheids; (7) a probable absence of bars of Sanio from many of the tracheids; (8) an increase in the number of rays in the gall wood; (9) a tendency toward the production of multiseriate rays; (10) ray tracheids which are transitional between those of hard and soft pines; (11) the presence of a balled or whorled arrangement of tracheids in the tangential sections; (12) a great increase in the number of resin canals in the gall wood, but no such increase in the uninfected wood close by. The examination of this gall has revealed so many points of anatomical interest that a further study of this subject seems to be worth while. On this account the author expects from time to time to issue other papers on the anatomy of *Peridermium* galls on pines and other conifers." It remains for someone to make a study of the very early stages of this and many other abnormal plant growths.

ROSEN[9] has made a study of the histology of the grape leaf gall. The author has made a study of this gall from its very earliest stages to its maturity. He summarizes his results as follows: "(1) the *Phylloxera vastatrix* leaf gall starts to develop on embryonic bud leaves; in 24 hours the insect produces a depression at the periphery of which hairs are formed on the upper surface of the leaf; the depression is due to a lessened growth of the attacked mesophyll; (2) after 3–4 days of insect attack the lower half of the leaf tissue which surrounds the portion in which the proboscis is inserted has proliferated enormously; the whole thickness of the leaf in the region immediately around the proboscis shows no proliferation; that portion of the leaf which is beneath the insect does not proliferate, but the upper half at the sides of the insect grows and forms the walls of a large insect cavity; upper epidermal cells and several layers of mesophyll cells in the portion of the gall below the insect show peculiar thickening and dissolution of their cell walls; (3) gall development depends upon leaf development; when the leaf reaches its maximum size, after 12–15 days of development, the gall becomes mature; (4) a mature gall shows but slight cuticular development and very few stomata; the mesophyll is a huge mass of compact, thin-walled, partly empty cells, some of which are undersized, and others enormously elongated; the vascular elements are scattered by wedges of parenchyma cells; many unicellular and multicellular hairs grow out from the gall; (5) chemical work on this gall shows it to be a structure in which anabolic processes are lacking, and in which large amounts of simple sugars and simple proteins are present; (6) the development of this gall does

[9] ROSEN, HARRY R., The development of the *Phylloxera vastatrix* leaf gall. Amer. Jour. Bot. 7:337–360. 1916.

not seem to support the theory that the insect injects some chemical into the leaf which causes gall formation; (7) intumescences produced by chemical sprays result from entirely different kinds of hyperplastic responses than hyperplastic gall growth; (8) the investigation establishes the fact that the proboscis may pass through the entire thickness of the leaf; (9) the insect remains fixed, and that portion of the leaf in which the proboscis is fixed is marked by lack of growth as compared with the huge outgrowths which surround it; (10) the continuous sucking action by the insect at one fixed point for fifteen days is believed to be the initial stimulus for gall development."

Another very interesting paper is by WELLS,[10] who has made a study of the galls of our common American hackberry. The purpose of the paper as stated by the author is as follows: "(1) to present a survey of the known insect and mite galls of *Celtis occidentalis* L.; (2) to elucidate the history of the normal gall-bearing parts of the hackberry and that of the galls; (3) to study comparatively the structures treated, pointing out any significant conclusions and generalizations that may be attained in such a study." The author gives excellent descriptions of the external and histological character of the galls and concludes the paper with the following summary: "(1) there are 17 known species of zoocecidia occurring on *Celtis occidentalis*, belonging to 4 orders of arthropods (Acarinae 1, Lepidoptera 1, Hemiptera 5, Diptera 10); all are heteroplasias, that is, those forms of hyperplasias (abnormal increase in size through cell proliferation) whose cells and tissues differ from the normal; all, be it noted, are built up on the basis of the same germ plasm, namely, that of the single species of the plant mentioned; (2) the acarinous and lepidopterous galls are kataplasmas of those forms of heteroplasias whose cells and tissues do not vary widely from the normal; each shows specific and characteristic inhibition of differentiation; (3) the hemipterous and dipterous galls are prosoplasmas of those forms of heteroplasias whose cells and particularly whose tissue forms differ fundamentally from those of the normal parts; (4) in the prosoplasmas the types of cells found are closely comparable to those of the normal plant parts, but the tissue forms discovered are fundamentally new; no analogous structure forms are to be found in the tissues of the normal plant or its allies; (5) in the dipterous prosoplasmas, since the gall's specific tissue form characters are related to the species of insect, we have the unique case of the 'overlapping' of the hereditary constitution of an animal on that of the plant in the sense that factors associated with the insect determine the form character locally, rather than those normally associated with the plant's germ plasm; these latter plant factors suffer suppression; (6) it is suggested that in the field of zoocecidiology we probably have a unique place, heretofore unrecognized, to attack the problem pertaining to the mechanism used in the expression of hereditary characters." The paper is well illustrated.—MEL T. COOK.

[10] WELLS, BERTRAM W., The comparative morphology of the zoocecidia of *Celtis occidentalis*. Ohio Jour. Sci. **16**: 249–290. 1916.

Transpiration studies.—Among the more recent devices for the investigation of the conditions affecting transpiration is the porometer devised by DARWIN,[11] which has attracted the attention of several workers, leading to improvements by BALLS[12] and by JONES[13] resulting in self-recording instruments. KNIGHT[14] then somewhat simplified the device, and later, assisted by LAIDLAW,[15] produced an automatic instrument that is probably better than its predecessors for most forms of stomatal investigations. All agree in measuring the stomatal opening by the rate at which air passes through the stomata with a given pressure. A rather careful study by KNIGHT[16] of the methods to be employed in avoiding errors in the use of the porometer is suggestive to future investigators in this field. Among the interesting results obtained by this method there may be mentioned those of DARWIN, and of LAIDLAW and KNIGHT, who found indications that upon severing a leaf from a stem and allowing it to wilt, a temporary opening of the stomata immediately preceded the closure accompanying wilting.

In a recent investigation TRELEASE and LIVINGSTON[17] have made a comparison between the porometer and the standardized cobalt chloride paper methods, and have obtained results showing a general agreement of data from the two. In the daily march of transpiring power the two are in close accord during the morning hours up to about 8:00 A.M., but from that hour until 11:00 A.M. the porometer index continues to increase, while the cobalt paper index tends to decrease. After 11:00 A.M. the influence tending to decrease becomes evident in the porometer index also. This is taken to indicate that the porometer measures the diffusive capacity of the stomata, but fails to take into account other influences affecting foliar transpiring power. The divergence in the two records, therefore, may be an index of non-stomatal influences upon transpiration. On account of the limited data, these workers are not inclined to press this conclusion, but it appears to be an extremely probable suggestion.

[11] DARWIN, F., and PERTZ, D. F. M., A new method of establishing the aperture of stomata. Proc. Roy. Soc. London B **84**:136–154. 1911.

[12] BALLS, W. L., The stomatograph. Proc. Roy. Soc. London B **85**:33–44. 1912.

[13] JONES, W. N., A self-recording porometer and potometer. New Phytol. **13**: 353–364. 1914.

[14] KNIGHT, R. C., A convenient modification of the porometer. New Phytol. **14**:212–216. 1915.

[15] LAIDLAW, C. G. P., and KNIGHT, R. C., A description of a recording porometer and a note on stomatal behavior during wilting. Ann. Botany **30**:47–56. *figs.* 3. 1916.

[16] KNIGHT, R. C., On the use of the porometer in stomatal investigation. Ann. Botany **30**:57–76. 1916.

[17] TRELEASE, S. F., and LIVINGSTON, B. E., The daily march of transpiring power as indicated by the porometer and by standardized hygrometric paper. Jour. Ecology **4**:1–14. *figs.* 2. 1916.

An investigation upon a much larger scale, resulting in an abundance of data, is reported by BRIGGS and SHANTZ.[18] It was carried on at Akron, Colorado, and the transpiration was determined by weighing plants potted in sealed cans upon the automatic scales recently described by the same authors.[19] Solar radiation, wet-bulb depression, evaporation, air temperature, and wind velocity were also measured, and the relationship between these physical factors and transpiration was shown. The plants employed were wheat, oats, sorghum, rye, alfalfa, and *Amaranthus retroflexus*, the hourly rate throughout the entire day being determined, the number of determinations ranging from 6 for *Amaranthus* to over 40 for alfalfa. The resulting data are expressed in tables and graphs which also serve to express their relationship with the physical factors. Correlation coefficients and method of least squares are also used to analyze these relationships and give some interesting results. Space permits the citing of their final conclusion only, to the effect that their results agree with those of other investigators that plants under conditions of high transpiration do not respond wholly as free evaporating systems, even if bountifully supplied with water. It is interesting to note that none of the plants here studied show the mid-day drop reported by TRELEASE and LIVINGSTON, by SHREVE, and by other observers at the Desert Laboratory.

MUENSCHER[20] has used the method of determining water loss by weighing and then making counts and measurements of the number and size of the stomata of *Phaseolus*, *Ricinus*, *Zea*, *Primula*, *Impatiens*, *Pelargonium*, *Triticum*, and *Helianthus*. He found no constant relation between the number and size of stomata in relation to unit area of leaf surface and the amount of transpiration. He also concludes that the amount of transpiration is not governed entirely by stomatal regulation. His work, however, does not show any explanation for any other control.

In one of the most recent publications upon this subject, by BAKKE and LIVINGSTON,[21] data are given upon the daily march of foliar transpiring power of different leaves of plants of *Xanthium* and *Helianthus*. These serve to emphasize the fact that the control of foliar transpiration by the plant is a complex one, especially as there is a great range in transpiring power among the different leaves of the same plant with considerable variation in time of the diurnal maxima. No very definite relation is established between age of leaves and their behavior, except that the oldest ones always show a low daily range of

[18] BRIGGS, L. J., and SHANTZ, H. L., Hourly transpiration rate on clear days as determined by cyclic environmental factors. Jour. Agric. Research **5**:583–649. 1916.

[19] ———, An automatic transpiration scale of large capacity for use with freely exposed plants. Jour. Agric. Research **5**:117–132. 1915.

[20] MUENSCHER, W. L. C., A study of the relation of transpiration to the size and number of stomata. Amer. Jour. Bot. **2**:449–467. 1915.

[21] BAKKE, A. L., and LIVINGSTON, B. E., Further studies on foliar transpiring power in plants. Physiol. Researches **2**:51–71. 1916.

transpiring power and usually low maximum index values. In addition to the transpiration data, this paper contains a description of an improved apparatus for providing a standard evaporating surface.—GEO. D. FULLER.

Fossil cycads.—The second volume of WIELAND's[22] memoir on American fossil cycads represents a large amount of additional work on material with structure preserved, and in particular of a new monocarpic trunk from the Black Hills discovered by Dr. N. H. DARTON. It is replete with admirable line drawings and half-tones representing both external form and internal structure. The material is in addition illustrated by 58 superb plates in heliogravure. The whole constitutes an achievement of which American paleobotany may well be proud.

Although the volume is described as systematic in its contents, it contains much that is of interest to the anatomist and the evolutionist. Considerable space is devoted to the anatomy of trunks of cycadeoidean forms, and the fact that the fibrovascular tissues are much more woody than in the living representatives of the cycads is emphasized. This is the consequence of the narrow rays and the sparse parenchyma, both features of contrast to the living cycadean cylinders. The author apparently has not found in American Mesozoic material the interesting reduplication of the central cylinder recently described by STOPES in a publication of the British Museum. This situation is interesting as it tends to discredit the hypothesis of WORSDELL that the reduplication of the cylinder in cycads is a vestige of the complex system of fibrovascular bundles found in certain species of *Medullosa*, etc. The situation in fact is comparable rather with that found in vines, and it is interesting to note in this connection that it is not improbable that the cycadeoidean genus *Anomozamites* was a climbing plant. The author emphasizes the statement that the mucilage cavities of the cycadeoidean forms were isolated cysts and did not constitute a system of canals as in living cycads.

Certain interesting statements are recorded in regard to the leaves, although most of these represent only elaborations of facts already known. The leaf trace departs from the cylinder as a large horseshoe-shaped strand which passes directly toward the leaf base, breaking up into numerous bundles in transit. This situation is in marked contrast to conditions in the living genera where numerous strands take their exit from the cylinder for each leaf and pursue a circuitous course through the cortex toward the leaf base. It is obvious that the cycadeoidean forms, so far as their anatomy is known, were unilacunar, that is, there was a single gap in the cylinder of the stem for each foliar supply; while in the living Cycadales the vascular system of the leaf is multilacunar. The cycadeoidean condition is obviously more primitive, as it is found in the reproductive axis and occasionally in the seedling of living forms. The ana-

[22] WIELAND, G. R., American fossil cycads, Vol. II, Taxonomy. Carnegie Inst. Washington, Publication 34. 1916.

tomical conditions in the Cycadophyta as regards the number of foliar gaps for the vascular supply of the leaves illustrate the danger of using the number of leaf gaps as a phylogenetic criterion, as has recently been attempted in the case of the dicotyledons. The leaf supply of the cycadeoidean forms was distinguished from that in the petiole of existing cycads by the strong development of secondary growth in the bundles on the upper side.

The reproductive structures are considered in some detail in the light of additional facts. The reviewer, however, expresses a regret, which will doubtless be common to those interested in the evolutionary history of the seed plants, that so little further information has been secured in regard to the crucial apical region of the seed. The author still maintains his earlier position in regard to the cycadeoidean origin of the angiosperms. Although he is supported in this view by a number of eminent European paleobotanists, perhaps it is open to question whether a hypothesis which finds little valid support in the anatomical organization of either the reproductive or vegetative structures will in the long run prove acceptable. The Goebelian character of the author's morphology is everywhere apparent, but most strikingly perhaps when he ventures to compare the seed of the Pteridosperm with an angiospermous flower. Surely this is carrying the Goebelian definition of an organ as the tool of a function to its logical *reductio ad absurdum*.

The memoir under discussion contains a wealth of facts to which it is impossible to do justice in a review. It will rank with those of BERRY as a most notable recent contribution to American mesozoic paleobotany.—E. C. JEFFREY.

The cohesion theory.—The cohesion theory of sap ascent has received much attention in recent years, and much supporting evidence has been brought out; but JOST[23] does not agree with RENNER that it is practically substantiated, and that all we need to do now is to find out where the cohering water columns are located. He believes much experimental work is still necessary to determine whether this theory is correct. Proceeding from early experiments of SACHS and others, and using mainly such plants as *Sanchezia*, *Cobaea*, *Biota*, and *Chamaecyparis*, he has made a quantitative study of water delivery by the basal portion of decapitated plants, as compared with the transpiration need of the top before and after cutting. The principal experiments attempt to determine the influence of suction upon the rate of water delivery by the root, and to determine whether continuous negative pressures can be maintained by a transpiring plant. As suction and pressures of only one or two atmospheres were used, the experiments seem to the reviewer little adapted really to test the cohesion theory; and considerable space is occupied in giving single examples of unsuccessful experiments of various sorts, which

[23] JOST, LUDWIG, Versuche über die Wasserleitung in der Pflanze. Zeitschr. Bot. **8**:1–55. 1916.

will have value no doubt in preventing useless attempts along the same lines. However, they provide JOST the opportunity to discuss the cohesion theory and to present his own views of it.

The actual results add little that is new. He found that suction on the root causes an increase in water delivery, especially in plants which normally exude sap on being cut, and that greater suction causes a greater root excretion of water than low suction. But there seems to be no proportion between amount of suction and rate of water delivery, as should be the case if the root acts merely as a filter in water intake. The maximum suction possible with an air pump could never cause a delivery sufficient to cover even a moderately estimated transpiration need. Completely surrounding the root with water, or replacing the atmosphere about the roots with hydrogen, or excessive cooling of the roots, leads to noticeable decrease of water delivery, even with strong suction.

Tensions existing in the water columns of the intact plant were demonstrated by the rapid intake of water by freshly cut tops, although the plants previously had been kept in condition of low transpiration. Suction on the cut end of the top, or pressure exerted upon it, produces only a temporary decrease or increase respectively in water intake by the top. It was found that plants could continue transpiration essentially undiminished at real negative pressures of 15–25 cm.

JOST comes to the conclusion that, even in low plants like *Cobaea*, *Chamaecyparis*, etc., just as in tall trees, very considerable negative pressures must exist, if we assume that the osmotic pull of transpiring leaves must pull in sufficient water through a passive filter-like root.

In the concluding section he questions whether it is possible for high negative pressures to exist continuously in the stems of plants, and proceeds to answer the question by subjecting stem tissues to high gas pressures. In *Ficus Carica* he found all the vessels easily penetrated by air, this experience running counter to the recent work of RENNER and HOLLE, which shows that there may be two kinds of vessels present, storage and conducting, the latter being more or less impermeable to air, and providing the cohering water columns. In such a case as *Ficus*, JOST thinks that those who hold to the cohesion theory must suppose either that there are no cohesion phenomena in plants with nothing but tracheae, or that certain vessels remain with cohering water columns by pure accident, or that in closed vessels entirely different conditions obtain from those which have been cut. The question of unbroken columns is vital to the cohesion theory, and those who adhere to it must expect to be called upon to prove the existence of cohering columns of water which can remain unbroken under the reduced or negative pressures involved in normal transpiration. The conservative view of so prominent an authority on plant physiology will help us to maintain a balanced perspective with reference to this important problem.—CHARLES A. SHULL.

Genetical investigations of maize endosperm.—FUJII and KUWADA[24] have noted chemical differences between the red and the purple pigments of the aleurone cells of maize, as indicated by differences in their solubility in alcohol and in 1 per cent aqueous solution of sodium carbonate, and in their color reactions with acids and alkalies. They state that the two pigments occur either separately or together in the same seed. The latter fact, if substantiated, should prove of interest to geneticists working with maize. The authors suggest that variations in intensity of aleurone color may be accounted for in part by the triploid nature of the endosperm, whereby reciprocal crosses may differ in having either 1 or 2 doses of the dominant factor concerned and F_2 seeds differ in having either 1, 2, 3, or no doses. A cumulative effect of dominant factors is assumed. They are apparently in error in attempting to apply the same assumption to red color of wheat, where, so far as known to the reviewer, the color is in the pericarp (diploid) rather than in the endosperm.

The genetical significance of the triploid nature of maize endosperm was earlier pointed out by HAYES and EAST[25] in reporting results of crosses between races with corneous and with floury endosperm. In reciprocal crosses between flinty and floury varieties xenia did not occur. In F_2 a 1:1 ratio was obtained whether the F_1 was self-pollinated or cross-pollinated by either the flinty or the floury parent. A half of each class of seeds resulting from self-pollination bred true and the other half again segregated. When F_1 was cross-pollinated by the flinty parent, all the corneous seeds bred true and all the floury ones proved to be hybrid, while the reverse was true when F_1 was crossed back to the floury parent. Two hypotheses are offered to account for the results: (1) the endosperm develops from the fused polar nuclei without double fertilization, or (2) the two polar nuclei dominate the single second male nucleus. A plant, pure for white endosperm but hybrid for endosperm texture, pollinated by a pure yellow corneous seeded race, gave a 1:1 ratio of corneous and floury seeds, all of which were yellow, thus demonstrating double fertilization and indicating the second hypothesis, that two doses of a factor for floury endosperm dominate one dose of the corneous factor and vice versa. Crosses of popcorn with both floury and dent types gave results more difficult of analysis, owing in part, the authors suggest, to differences in seed size, but two independent factor-pairs are indicated in at least some of the cases. It is also thought that two factor-pairs are concerned in the inheritance of sharp points characteristic of rice pop-corn.—R. A. EMERSON.

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[24] FUJII, KENJIRO, and KUWADA, YOSHINARI, On the composition of factorial formula for zygotes in the study of inheritance of seed characters of *Zea mays* L., with notes on seed pigments. Bot. Mag. (Tokyo) **30**:83–88. 1916.

[25] HAYES, H. K., and EAST, E. M., Further experiments on inheritance in maize. Conn. Agric. Exp. Sta. Bull. no. 188. pp. 31. *pls.* 8. 1915.

Genetics of flax.—Miss TAMMES[26] has made a genetical study of the flower characters of 6 varieties of the common flax, *Linum usitatissimum*. These varieties consisted of 3 dark blue, 1 light blue, and 2 white varieties. Besides the color of the flower, with which she worked chiefly, she studied the color of the anthers, the color of the seeds, the shape of the petals, the color of the veins in the petals, and the number and viability of the seeds produced. These latter characters she finds correlated with the color of the flower and dependent upon the same factors. The several varieties are described and their genetic formulae given, after which the author presents in tabular form the expected ratios and the observed results in the second and third generations. She concludes that the blue color is the result of two complementary factors, *B* and *C*. The presence of these two factors alone produces the light blue flowers, and the dark blue is brought about by the action of an intensifying factor *A* cooperating with *B* and *C*. Unless both *B* and *C* are present the flower will be white. The factor *A* acts as an intensifier only on the light blue of the petals and has no effect on the color of the anthers, on the color of the seed, or on the color of the veins in the petals. The factor *B* is not only one of the necessary factors for the production of the blue flower color, but even without the cooperation of *C* brings about the blue color of the anthers and the brown color of the seeds, prevents the crinkling of the petals which, were it not present, would be caused by the presence of *C*, and overcomes the tendency of *C* to lessen the number and viability of the seeds. The factor *C*, besides producing, with *B*, the blue color of the flower, brings about, when in a homozygous condition, a deeper pigmentation of the veins in the petals; and causes, when *B* is absent, a crinkling of the petals and a lessening in the number and viability of the seeds. In respect to the color of the anthers, which results from the presence of *B*, it is pointed out that although the 6 varieties studied are in agreement with the interpretation given, there is a variety, which has not yet been studied, that has blue flowers and *yellow* anthers. As this is contrary to the conclusions arrived at from the 6 varieties investigated, the author suggests that the factor *B* may be, not a single unit, but a complex, with some essential part or factor lacking in the variety with blue petals and yellow stamens. On the other hand, *B* may be a unit and the blue anthers may be lacking because some other necessary factor besides *B* is lacking in that variety. An investigation of this problem is promised.—BEN C. HELMICK.

Physiological temperature and moisture indices.—In extending his studies of the derivation and use of indices of temperature in relation to plant growth, LIVINGSTON[27] distinguishes 3 classes of such indices. The first is the sum-

[26] TAMMES, TINE, Die genotypische Zusammensetzung einiger Varietäten derselben Art und ihr genetischer Zusammenhang. Extrait Recueil Trav. Bot. Néerland. **12**:217–278. 1915.

[27] LIVINGSTON, B. E., Physiological temperature indices for the study of plant growth in relation to climatic conditions. Physiol. Researches **1**:399–420. *figs.* 4. 1916.

mation of the daily mean temperature, above a certain fixed minimum, throughout the growing season. Such indices of temperature efficiencies for plant growth have been used largely by phenological students, notably in MERRIAM's "law of temperature control." An advance upon this method was suggested by LIVINGSTON,[28] based upon the supposition that growth rate may follow the chemical principle of van't Hoff, doubling with each increase of temperature of 10° C., and the present publication proposes to give the indices a value based upon physiological experiment. LEHENBAUER'S[29] recent experiments upon the growth rate of maize seedlings at different temperatures affords data for the derivation of these indices which surpass those formerly proposed in taking account of the recognized principle of temperature minima, optima, and maxima; and also in showing a much greater rate of increase of index value with rising temperature between 2° and 32° C. Charts showing the climatic zonation of the United States according to each of the 3 classes of indices are suggestive and interesting for study and comparison. The third method clearly surpasses the others in correctness of principles involved, and its indices are used by the same author[30] in deriving a single index for both temperature and moisture. As a measure of the moisture conditions, the ratio of annual rainfall to annual evaporation as suggested by TRANSEAU is used, and this ratio is multiplied by the summation index of temperature efficiency for the same period, and the product is the proposed moisture-temperature index. The general scheme is a good one, and the resulting zonation of the United States is interesting in spite of the utter inadequacy of the evaporation data. It may be doubted also whether this rainfall evaporation ratio expresses the moisture conditions which determine plant growth as well as the soil moisture-evaporation ratio suggested by the reviewer. It is true that here again the lack of data will prevent the effective use of this ratio for years to come.—GEO. D. FULLER.

Taxonomic notes.—COLLINS and HOWE,[31] in studying specimens of red algae from Bermuda, southern Florida, and North Carolina, have recognized 4 new species of *Halymenia*.

SAFFORD[32] has published *Desmopsis* as a new genus of Annonaceae, to include 5 species from Mexico, Panama, and Costa Rica, that differ in several important characters from the Old World *Desmos* (*Unona* Vahl).

[28] LIVINGSTON, B. E., BOT. GAZ. **56**:349–375. 1913.

[29] LEHENBAUER, P. A., Growth of maize seedlings in relation to temperature. Physiol. Researches **1**:247–288. 1914.

[30] LIVINGSTON, B. E., A single index to represent both moisture and temperature conditions as related to plants. Physiol. Researches **1**:421–440. *fig. 1*. 1916.

[31] COLLINS, F. S., and HOWE, M. A., Notes on species of *Halymenia*. Bull. Torr. Bot. Club **43**:169–182. 1916.

[32] SAFFORD, W. E., *Desmopsis*, a new genus of Annonaceae. Bull. Torr. Bot. Club **43**:183–193. *pls. 7–9. fig. 1*.

In the last number of HOOKER's *Icones Plantarum* (V. 1:*pls. 3051–3075*, June 1916), the following new genera are described and figured: *Pappobolus* Blake (Compositae), *Mischopleura* Wernham (Ericaceae), *Neowollastonia* Wernham (Apocynaceae), *Dalzielia* Turrill (Asclepiadaceae), *Eriolopha* Ridley (Zingiberaceae), *Chloachne* Stapf, *Uranthoecium* Stapf, and *Danthoniopsis* Stapf (Gramineae). In addition to these 8 new genera, 7 new species are described.

KOIDZUMI,[33] in continuing his studies of Castanaceae, has recognized *Synaedrys* Lindl as a genus, extending it considerably, and has included under it 150 species transferred from *Quercus*. He also lists 234 species as remaining under *Quercus*.

RIDDLE[34] has presented a complete list of the known lichens of Bermuda, including 86 species representing 36 genera. New species are described in *Thelidium*, *Anthracothecium*, *Opegrapha*, *Bilimbia*, *Psorotichia*, and *Collema*.

WEST,[35] in continuation of his studies of algae, has described a new marine genus of the Volvocales (sub-family Carterieae), naming it *Platymonas*. He also describes new species in *Chlamydomonas* (2) and *Pteromonas*.—J. M. C.

Eocene floras.—The geographic area covered in the recent monograph by BERRY[36] is the mainland south of latitude 41 and east of longitude 100. The Antillean and Mexican regions are not included even for comparison on account of meager information in regard to them. The memoir is monumental in its character, consisting of nearly 500 quarto pages and 117 plates. A few ferns and monocotyledons are described, and no conifers. Most of the illustrations represent impressions of dicotyledonous leaves. The only anatomical illustrations are of a *Cupressinoxylon* and a *Laurinoxylon*, which are of the conventional and vague nature that too often characterizes such illustrations in publications of the U.S. Geological Survey. Apparently the Survey either should not publish anatomical data at all or intrust their preparation to some one equipped with a modern anatomical training. An important and valuable feature of the work is the attempt to correlate the presence of fossil forms with the principles of phytogeography. This appears to be very well done and is not open apparently to the grave objections which present themselves in the case of the conifers of the Mesozoic, which for the most part have been wrongly identified from their impressions and consequently cannot be used safely in

[33] KOIDZUMI, GENICHI, On the classification of Castanaceae. II. Bot. Magazine (Tokyo) **30**:185–215. 1916.

[34] RIDDLE, LINCOLN W., The lichens of Bermuda. Bull. Torr. Bot. Club **43**:145–160. 1916.

[35] WEST, G. S., Algological notes. XVIII–XXIII. Jour. Botany **54**:1–10. *figs.* 7. 1916.

[36] BERRY, E. W., The Lower Eocene floras of southeastern North America. U.S. Geol. Survey. Professional paper 91. Washington. 1916.

discussing geographical distribution. The author sets a high example for American systematic paleobotanists. It is to be hoped, however, that the paleobotanical activities of the U.S. Geological Survey will not in the long run be confined to the systematic side, but that they will be extended, as has already been done in the case of European countries, to the crucially important although less abundant structural remains.—E. C. JEFFREY.

Lower Eocene plants.—BERRY[37] has published an extensive paper on the plants of the Lower Eocene of southeastern North America, being the result of several years of work on the fossil plants of the southern coastal plain. Naturally, much of the report deals with the stratigraphic relations illustrated by the plants, but the systematic descriptions are of great botanical interest. The orders represented, 34 in number, range from Pyrenomycetes to Rubiales, but 29 of the orders are angiosperms. *Caenomyces* is a new genus of Pyrenomycetes, including 6 species. The pteridophytes are represented by 5 new species, and *Meniphylloides* is proposed as a new genus of ferns. The gymnosperms are represented by 2 new species, one in *Zamia* and the other in *Anthrotaxis*, while 4 new species, representing as many genera, belong to the monocotyledons.

The bulk of the report, however, deals with the dicotyledons, 228 new species being described, distributed among 96 genera, among which are 7 new genera as follows: *Paraengelhardtia* (Juglandaceae), *Knightiophyllum* (Proteaceae), *Dalbergites* (Leguminosae), *Sterculiocarpus* (Sterculiaceae), *Bombacites* (Bombaceae), *Dillenites* (Dilleniaceae), and *Ternstroemites* (Ternstroemiaceae). One of the marked features in the composition of this dicotyledonous flora is the abundance of leguminous plants, of which 53 new species are described, 12 of which, for example, belong to *Cassia*. In addition to the new species assigned definitely to recognized families, 14 new species are described under form genera of uncertain relationship.—J. M. C.

Conjugate nuclei in Ascomycetes.—In a brief article, Miss WELSFORD[38] notes the fact that conjugate nuclei are common in the hyphae of well nourished mycelia of *Botrytis cinerea* and *Sclerotinia Libertiana*. In poorly nourished mycelia the paired nuclei are absent, as the nuclei under such conditions have time to move considerable distances apart before successive divisions occur. Miss WELSFORD observes that if conjugate nuclei occur generally in the mycelium of Ascomycetes, their presence in the ascogenous hyphae does not have the sexual significance usually attributed to it.—H. HASSELBRING.

[37] BERRY, E. W., The Lower Eocene floras of southeastern North America. U.S. Geol. Survey. Professional paper 91. pp. 481. *pls. 117. figs. 16.* 1916.

[38] WELSFORD, E. J., Conjugate nuclei in the Ascomycetes. Ann. Botany **30**:415–417. *figs. 4.* 1916.